Figure 16. The prevalence of *Triaenophorus nodulosus* in sticklebacks of different sizes collected by seining (S), trapping (M), or recovered from stomachs of trout (T) and of pike (P)

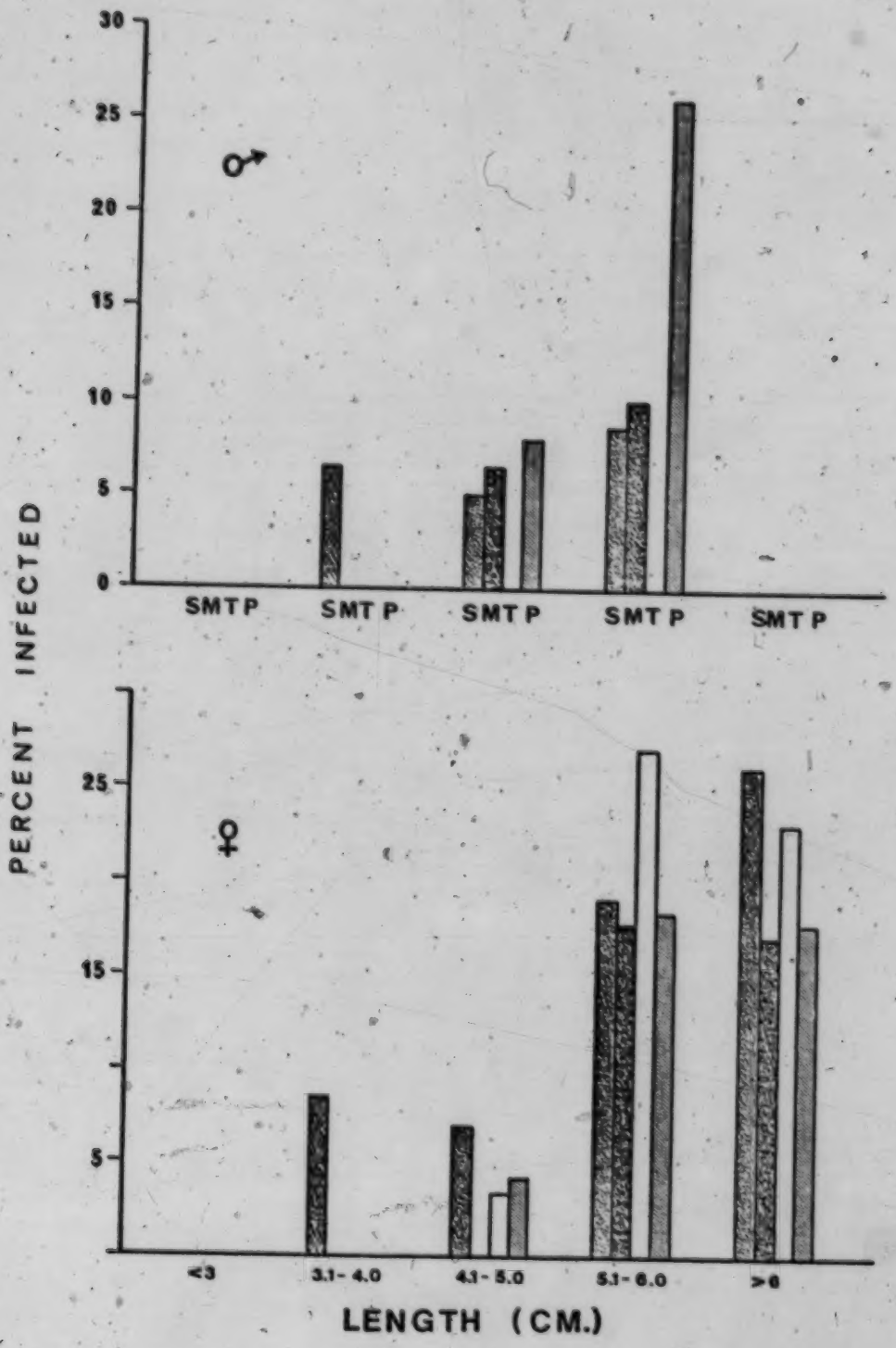
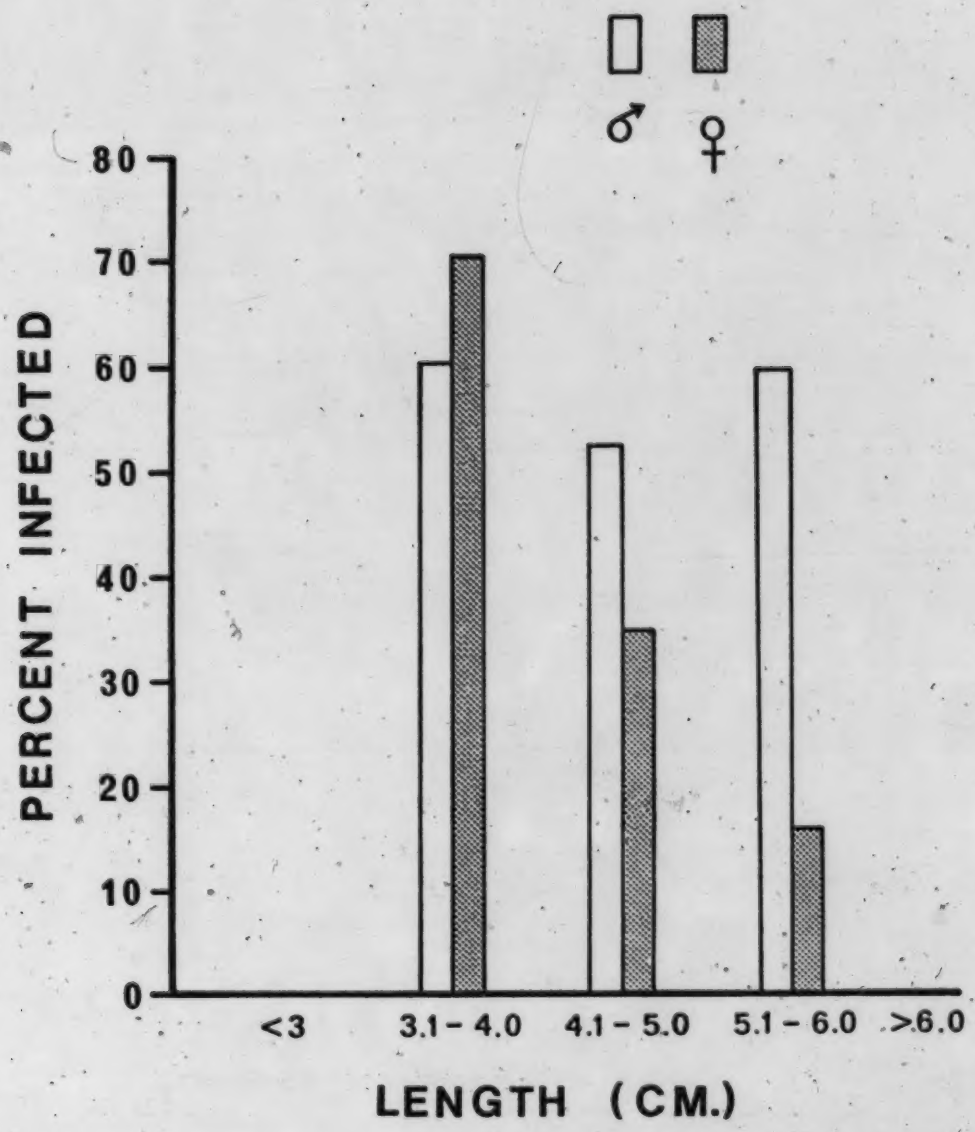

30
25
20
15
10
5
0
♂
SMTP
SMTP
SMTP
SMTP
SMTP
PERCENT INFECTED
25
15
5
♀
<3
3.1-4.0
4.1-5.0
5.1-6.0
>6
LENGTH (CM.)

Figure 17. The prevalence of *Schistocephalus solidus* in sticklebacks of different sizes collected by seining


♂
♀
PERCENT INFECTED
80
70
60
50
40
30
20
10
0
<3
3.1 - 4.0
4.1 - 5.0
5.1 - 6.0
>6.0
LENGTH (CM.)

trapped sticklebacks had a larger proportion infected with *Gyrodactylus* sp., *D. spathaceum*, *M. salmonis* and *E. auritus* than did shallow-water sticklebacks. These differences are partly, but not entirely, due to the larger fish in the sample of trapped sticklebacks (Figure 14). In part, they also may be due to behavioural changes in sticklebacks infected with *S. solidus*, which move into shallower, warmer waters (Lester, 1971). The presence of *S. solidus* was significantly negatively correlated with that of *D. spathaceum* and *M. salmonis* (and with that of *C. erraticus* and *T. nodulosus* as well) (Table 15).

Sticklebacks taken from the stomachs of trout or pike were frequently partly digested, making it difficult to tell whether the ectoparasitic monogenean, *Gyrodactylus* sp., or the metacercariae of *A. gracilis*, *C. erraticus* or *D. spathaceum* were present or not. Therefore, these four species have not been included in the following analyses.

Sticklebacks eaten by predatory fishes resembled those taken by minnow trap in size (Figure 14), and in having a low prevalence of *S. solidus* but high prevalences of *E. auritus* and *M. salmonis* (Table 14). They had higher mean numbers of individuals per fish, but lower indices of diversity, than trapped (or seined) sticklebacks (Table 14).

Discussion

Each species of fish examined showed a distinct preference for specific, generally different food items. As a result, each species has a specific food niche within the ecosystem.

Whitefish feed in the benthic zone, mostly on *P. affinis*, tendipedids, and sphaeriids. These three items also made up the majority of their food in other studies in lakes where cisco were present (Koelz,

Table 15. Concurrent infections between *Schistocephalus solidus* and other larval parasites in ninespine sticklebacks collected by seining

Number of fish infected with:	*Schistocephalus solidus*		
	Present (322)	Absent (484)	Significance*
Cotylurus erraticus	128	226	HS (neg)
Diplostomum spathaceum	164	379	HS (neg)
Triaenophorus nodulosus	17	77	HS (neg)
Metechinorhynchus salmonis	22	112	HS (neg)
Apatemon gracilis	41	60	NS
Eubothrium spp.	31	36	NS
Raphidascaris sp.	0	2	NS

*HS - highly significant ($P < 0.001$) (G-statistics, Sokal and Rohlf, 1969). NS - not significant.

1929; Hart, 1931; Rawson, 1959, 1960; Koshinsky, 1965; Rechahn, 1970); in lakes where cisco were not present they also fed extensively on plankton (Bidgood, 1973). The general conclusion has been that their food habits depend on the availability of different items within the food niche they can occupy.

Cisco feed primarily on plankton, or on organisms that periodically enter the plankton, such as *Mysis*, amphipods, or aquatic insects (Pritchard, 1931; Dryer and Beil, 1964). They normally feed in the epilimnetic zone.

Lake trout are limited to cold water; in the summer, they occupy the hypolimnion, where they feed mainly on fish, mostly cisco. In the spring, with cooler water, they feed mainly on sticklebacks which begin to congregate, soon after ice break-up, in the shallow water (Roberts, 1975). In most studies, cisco appear to be the preferred prey (Rawson, 1959, 1961; MacCrimnon and Skobe, 1970; Martin, 1970) but in Lake Ontario alewives (Dymond, 1928) and in Lake Superior smelt (Dryer *et al.*, 1965) were of primary importance, suggesting that availability is a major factor.

Pike are predators which occupy primarily the littoral zone, feeding almost exclusively on fish of whatever species are available (Lawler, 1965). In Cold Lake, they feed largely on sticklebacks, competing with trout in the spring, but not in the summer.

The types of food consumed by burbot depend on their size; those over 50 cm feed exclusively on fish, of whatever species of fish are available (Van Oosten and Deason, 1938; Clemens, 1951; Wagner, 1972), and those under 50 cm feed mainly on invertebrates (Clemens, 1951). Most of the burbot in my studies were less than 50 cm and had fed mainly

on invertebrates. They shared the benthic zone with whitefish and compete with them for *P. affinis* and, to a lesser extent, other amphipods.

Thus each of the larger native fishes has a special food niche, overlapping others only slightly. Young introduced coho also appear to have a separate food niche. In Cold Lake, as in Lake Michigan (Peck, 1974), or various lakes in Colorado (Klein and Fennell, 1969) or Wisconsin (Avery, 1973; McKnight and Serns, 1974), young coho fed mainly on insects. However, older coho usually, but not always, switch to a diet composed primarily of fish. In the ocean, fish comprise about 80 percent of their diet (Prakash, 1962); in the Great Lakes, the larger coho feed principally on smelt and alewives (Scott and Crossman, 1973). In Cold Lake, too, the larger coho (age class III) fed primarily on fish: 82 percent of those with food in the stomach had fed on fish, primarily sticklebacks and cisco. The food niche of the larger coho in Cold Lake, therefore, had a considerable overlap with those trout and pike. The limited food niche for older coho in Cold Lake may have contributed to the failure of this introduction.

In temperate lakes, temperature has a profound influence on the diet, rate of feeding and rate of digestion of the fish. Data, such as I have presented, on the proportion of stomachs containing food depend upon both the rate of feeding and the rate of digestion. There appears to be no information in the literature on the effect of temperature on these rates in the species of fishes I have examined, but Brett and Higgs (1970) have examined the effects of temperature on these rates in another cold-water fish, fingerling sockeye salmon. The situation appears to be complicated by temperature compensation in both feeding and

digestion rates, but primarily the former, at low temperatures. However, their data would suggest that maximum meal size is reduced at low temperature, and that the average meal would take about .33 days to digest at 1 C, about 6 days at 3 C, but less than 1 day at 15 C or above.

Although some whitefish and/cisco have food in their stomachs throughout the year, incorporation of the rates of digestion indicated by Brett and Higgs' work suggests that the rate of feeding is relatively low during the period of ice cover, that there is a tremendous increase in feeding after ice break-up when temperatures are rising, and that the fish are actively feeding throughout the summer, despite the high proportion of emptied stomachs. There appears to be evidence of reduced feeding prior to spawning, then increased feeding after spawning. These presumed feeding rates appear to correlate nicely with the observed numbers of *M. salmonis*, at least in whitefish.

The absence of any correlation between the diversity of foods and the diversity of parasites is not surprising; it appears to be due to a combination of three factors. First, the individual food items vary greatly in importance as intermediate or transport hosts for parasites. Amphipods are obviously very important, as are copepods and, to a lesser extent, fish. Molluscs, insects and mysids appear to be relatively unimportant.

Second, some food items that must have been eaten on the basis of the parasites recovered, were not found in the food habit studies. For example, no copepods were found in whitefish, but the significant numbers of proteocephalids indicate that copepods must have been eaten. Using similar arguments, Collins and Dechtiar (1974) deduced from the parasite fauna recovered from introduced kokanee salmon in Lake Huron

the kind of food items which might have been consumed by the salmon.

Third, even if several species of fishes ingest the same kinds of larval stages, host specificity can affect the kinds of parasites which will develop. *Gammarus lacustris*, the intermediate host of *C. stigmatura*, were eaten in substantial numbers by whitefish, cisco, coho and burbot; the first three harboured the nematode, burbot did not.

A fourth factor may also be involved. Larval parasites may change the behaviour of the infected intermediate host so that it becomes susceptible to predators feeding in one way, but not to those feeding in another way (Holmes and Bethel, 1972; Bethel and Holmes, MS). In that way, two predators feeding on the same intermediate host species could be feeding on different parts of the intermediate host's population, and acquire different parasites. The data presented earlier on sticklebacks taken by pike and trout indicate that these predators are feeding on a selected part of the stickleback population and get different parasites than surface-feeding birds would get. There is no evidence, however, that pike feed on a different part of the stickleback population or are exposed to different parasites than trout.

VI. PARASITES OF COHO

Fingerling coho salmon (age class II), raised from eggs in the Alberta Government hatchery at Raven Creek, were introduced experimentally into Cold Lake, Alberta, each spring from 1970 through 1972. I was able to study their parasites in 1971, when they were introduced in late June, and in 1972, when they were introduced in late April. Samples of fingerlings (57 in 1971, 23 in 1972, for a total of 80) were examined for metazoan parasites at the time of their release into Cold Lake; no parasites were found.

Very few parasites were found regularly in coho during their first summer in the lake; a few others were found sporadically (Table 16). More species (10) were encountered in the class II coho in 1972 than in 1971 (6), as might be expected from their longer residence in the lake. However, the mean number of individuals per infected fish did not differ significantly between years, and the mean number of species per fish was significantly less in 1972 than in 1971 (Table 16).

Almost all coho examined were infected with *M. salmonis* soon after entering the lake; it was the only parasite found regularly in both years. Populations of *M. salmonis* in the young coho appeared to be fairly similar in the two years through August, but were markedly higher in September and October of 1972, reflecting the considerably larger size of the fish taken in those periods (Table 17), many of which were large precocious males.

The two species of *Ergasilus* were abundant in young coho in 1971, but relatively scarce in 1972 (Table 16), accounting for the difference

Table 16. Comparison of the prevalence and mean intensity (in parentheses) of parasites acquired by coho salmon of age class II

Parasites	1971	1972
Crepidostomum farionus	4.6 (4.0)	4.8 (1.1)
Duphyllobothrium sp.**	0	5.5 (1.3)
Eubothrium spp.*	0	2.8 (2.3)
Proteocephalus spp.*	0	4.8 (7.1)
*Triaenophorus nodulosus***	1.5 (2.0)	4.1 (1.1)
Metechinorhynchus salmonis	100 (37.5)	98.6 (65.2)
*Pomphorhynchus bulbocolli**	9.2 (2.5)	2.1 (1.0)
*Neoechinorhynchus strigosum**	0	1.4 (3.0)
Ergasilus auritus	36.9 (4.9)	07.6 (5.5)
Ergasilus nerkae	93.9 (38.0)	16.6 (7.0)
No. examined[1] (n)	65	145
No. spp. (S)	6	10
Mean no. spp. ($\bar{S}$) (± S.E.)	2.45 (±0.09)	1.5 (±0.06)
Mean no. ind. per infected host ($\bar{N}$) (± S.E.)	75.4 (±5.45)	66.6 (±6.65)

[1]Excluding a total of 80 coho examined in both years before releasing, all were negative.

*Immature.

**Larval.

Table 17. The seasonal prevalence and mean intensity (in parentheses) of common parasites acquired by age class II coho salmon in 1971 and 1972. The coho were introduced into Cold Lake in late June, 1971 and late April, 1972. Values for S, $\bar{S}$ and $\bar{N}$ are for the entire parasite fauna.

Parasites		June	July	August	September	October
Metechinorhynchus salmonis	1971		100(26.5)	100(31.8)	100(39.3)	100(105)
	1972	87.5(35.7)	97.4(20.1)	100(38.4)	100(187.2)	100(243.5)
Ergasilus auritus	1971		25(1)	46.5(5.9)	7.1(10)	75(6)
	1972	12.5(40)	0	14.3(2.1)	0	0
Ergasilus nerkae	1971		0	100(29.5)	100(52.6)	75(34)
	1972	0	0	34.3(7.0)	0	0
No. examined	1971	0	4	43	14	4
	1972	8	38	70	20	9
Mean fork length (±S.D.)	1971		20.7(±1.5)	22.8(±0.22)	24.8(±0.76)	26.3(±0.65)
	1972	19.9(±1.16)	23.0(±0.44)	26.3(±0.39)	34.6(±0.85)	38.3(±0.6)
S	1971		3	7	5	3
	1972	3	1	8	7	2
$\bar{S}$	1971		1.50	2.65	2.29	2.50
	1972	1.50	0.97	1.79	1.55	1.11
$\bar{N}$±S.E.	1971		29.3(±7.9)	68.3(±5.2)	93.4(±11.3)	135(±42.0)
	1972	69(±26.1)	20.1(±3.1)	41.5(±6.2)	188.0(±20.5)	234.7(±33.1)

in $\bar{S}$ between years. For *E. nerkae*, the decrease in 1972 paralleled a similar reduction in the population of this parasite in cisco, but the population of *E. auritus* in cisco did not decrease in 1972 (Table 11). At least in 1971, *E. nerkae* appeared later, and reached peak populations later, than *E. auritus* (Table 17). This seasonal pattern is similar to that in cisco.

Relatively small numbers of overwintered age class III coho were recaptured, mainly in the fall when they returned to spawn in the Medley River. In general, these overwintered coho harboured more individuals of more species of parasites than did the younger coho (Table 18), including substantial populations of two species, *C. stigmatura* and *P. agubernaculum*, not encountered in the class II coho. Only *E. nerkae* was significantly more abundant in the younger coho. As in the younger coho, their parasite fauna was dominated by *M. salmonis*.

Overwintered coho captured in 1971 had significantly higher $\bar{S}$ and $\bar{N}$ than those captured in 1972 or 1973 (Table 19). The mean intensity of *M. salmonis* in 1971 was almost double that in 1972 or 1973; the same pattern was seen in cisco, but not in whitefish (Table 11). The two ergasilids were abundant in 1971, but sporadic or absent in the other two years. *E. nerkae* showed the same pattern in other hosts, but *E. auritus* (in cisco) did not. Of the other species which showed similar decreasing populations over the three years, the decrease in *C. stigmatura* was noteworthy, since populations of that parasite in whitefish increased over the same period (Table 11).

The general food habits of coho were covered earlier (section V, C). Because of the major differences in the parasite faunas of coho taken in different years, or of different ages, the diets of these groups

Table 18. The prevalence and mean intensity (in parentheses) of parasites acquired by coho salmon of age classes II and III

Parasites	Age class II	Age class III
Diplocotyle sagittata	0	1.3 (1.0)
Crepidostomum farionis	4.8 (2.0)	14.1 (2.3)
Cyathocephalus truncatus	0	2.6 (1.0)
Diphyllobothrium sp.**	3.8 (1.4)	7.7 (1.7)
Eubothrium spp.*	1.9 (2.3)	1.3 (12.0)
Proteocephalus spp.*	3.3 (7.1)	2.6 (19.0)
*Triaenophorus nodulosus***	3.3 (1.3)	1.3 (2.0)
Cystidicola stigmatura	0	15.4 (3.1)
Philonema agubernaculum	0	56.4 (19.3)
Metechinorhynchus salmonis	99.1 (57.5)	100 (532.9)
*Pomphorhynchus bulbocolli**	3.8 (2.3)	11.5 (1.2)
*Neoechinorhynchus strigosum**	1.0 (3.0)	0
Ergasilus auritus	16.7 (5.1)	16.7 (10.0)
Ergasilus nerkae	40.5 (29.2)	30.8 (26.7)
No. examined (n)	210	78
No. spp. (S)	10	13
Mean no. spp. ($\bar{S}$) (± S.E.)	1.79 (±0.06)	2.68 (±0.17)
Mean no. ind. per infected host ($\bar{N}$) (± S.E.)	68.1 (±4.88)	555.7 (±44.44)

*Immature.

**Larval.

Table 19. Comparison of the prevalence and mean intensity (in parentheses) of parasites acquired by 3-year old coho recovered in various years

Parasites	1971	1972	1973
Discocotyle sagittata	3.9 (1.0)	0	0
Crepidostomum farionis	30.7 (2.0)	7.7 (2.0)	2.6 (6.0)
Cyathocephalus truncatus	0	0	5.1 (1.0)
Diphyllobothrium sp.**	15.4 (1.8)	0	7.7 (1.7)
Eubothrium spp.*	3.9 (12.0)	0	0
Proteocephalus spp.*	0	0	5.1 (19.0)
Triaenophorus nodulosus **	0	0	2.6 (2.0)
Cystidicola stigmatura	30.8 (3.3)	23.1 (2.7)	5.1 (2.5)
Philonema agubernaculum	69.2 (37.6)	46.2 (2.0)	59.0 (9.7)
Metechinorhynchus salmonis	100 (782.6)	100 (404.4)	100 (407.9)
*Pomphorhynchus bulbocolli**	23.1 (1.1)	15.4 (1.5)	2.6 (2.0)
Ergasilus auritus	46.2 (9.8)	7.7 (13.0)	0
Ergasilus nerkae	92.3 (26.7)	0	0
No. examined (n)	26	13	39
No. spp. (S)	10	6	9
Mean no. spp. ($\bar{S}$) (± S.E.)	4.15 (±0.29)	2.0 (±0.25)	1.92 (±0.13)
Mean no. ind. per infected fish ($\bar{N}$) (±S.E.)	842.4 (±89.4)	407.3 (±94.1)	414.1 (±37.4)

*Immature.

**Larval.

were examined in more detail. Much of the following information comes from Roberts (1975), who studied the food of the coho I examined for parasites.

The major difference in the diets of the age class II coho between 1971 and 1972 appeared to be that a larger proportion had fed on fish and a much lower proportion had fed on insects in 1972 (Table 20). Older coho (age class III) fed even more extensively on fish (Table 20). Both features appear to be a function of size; Roberts (1975) analyzed the diets of class II coho by size (as measured by fork length), and found a decreasing dependence on invertebrates and an increasing dependence on fish as the coho increased in size.

DISCUSSION

When fish introduced into a new environment have been raised from eggs in a hatchery, such as the coho were, they do not transfer parasites characteristic of their native environment, although they may transfer new parasites, particularly protozoans or ectoparasites, acquired in the hatchery (Ivasik, Kulakovskaya and Vorona, 1969; Malmberg, 1972; Wootten, 1972). None of the coho examined before release had observable infections, suggesting that no new metazoan parasites, at least, were introduced. However, the very small numbers of *P. agubernaculum* in cisco did not appear to be sufficient to produce the heavy infections in over-wintered coho, suggesting the possibility that *P. agubernaculum* may have been introduced, in a cryptic early migratory stage, with the coho.

The young coho introduced into Cold Lake fed vigorously on insects, then later on fish, especially ninespine sticklebacks; the latter are a

Table 20. The prevalence of food in 1971 and 1972 age class II coho, age class II coho of both years, and age class III coho

	1971	1972	Combined years	
	II*	II	II	III
Whitefish	0	8.3	5.7	0
Cisco	4	1.9	2.5	46.4
Cyprinids	0	1.9	1.3	3.6
Walleye	0	1.0	0.6	0
Stickleback	30	38.0	35.4	32.1
Total Fish	34	51.1	45.5	82.1
Mysis relicta	2	0	0.6	0
Pontoporeia affinis	2	0	0.6	7.1
Gammarus lacustris	2	0	0.6	0
Total Amphipods	4	0	1.2	7.1
Total Crustaceans	6	0	1.8	7.1
Ephemeroptera	0	0	0	7.1
Odonata	16	0	5.1	0
Hemiptera	4	0	1.3	10.7
Trichoptera	74	54.6	60.8	7.1
Coleoptera	22	0	6.9	7.1
Diptera	18	2.8	7.6	0
Total Insects	134	57.4	81.7	32.0
Glossiphonidae	0	1.0	0.6	0
No. examined (n)	65	145	210	78
No. with food	50	108	158	28
No. food items (S(F))	10	8	14	8
Mean no. food items ($\bar{S}(F)$)	2.3	1.2	1.5	1.1
($\pm$S.D.)	($\pm$0.14)	($\pm$0.04)	($\pm$0.07)	($\pm$0.08)

* age class.

transport host for *M. salmonis*. The high prevalence and mean intensity of *M. salmonis*, and differences in these parameters in different years or age classes, were directly due to this vigorous feeding on sticklebacks. In contrast, kokanee (*Oncorhynchus nerka*) introduced into Lake Huron, which fed mainly on invertebrates and did not prey on other fishes (Collins, 1971), had much lower intensities of *M. salmonis* (Collins and Dechtiar, 1974) than did the coho in my study.

However, the high intensity of ergasilids could not be due to vigorous feeding by coho; it is probably a reflection of the behaviour of the young coho, which feed extensively in the upper surface waters of the lake in the early evening (Roberts, 1975). The recovery of large numbers of aerial insects from the stomachs of coho further strengthened this observation of preference for the upper surface. This preference, combined with the tendency of the nauplii of *Ergasilus* spp. to move to the surface at night (Bauer, 1959), produced a high potential for infection with ergasilids.

A greater number of parasite species were recovered from coho introduced in April, 1972, than those introduced in June, 1971; further, overwintered coho acquired more parasite species than those which had not overwintered, suggesting that the length of residence was an important factor.

Salmonid fish dominated the community of fish in Cold Lake and the parasite community was similarly dominated by those characteristic of salmonid fish. The parasites acquired by the introduced coho reflected that situation; 11 of the 14 species were primarily parasites of salmonids. The most abundant parasites were *P. agubernaculum*, *M. salmonis*, *E. auritus* and *E. nerkae*, all parasites of salmonids. Only three parasite species

(*T. nodulosus*, *P. bulbocolli* and *N. strigosum*) were acquired from non-salmonid fish, and of these, only *P. bulbocolli* was reasonably abundant.

There appear to be only two other reports of parasites in introduced coho. Klein and Fennel (1969) recovered only two species of parasites (*Crepidostomum farionis*, a parasite of salmonids, and *Proteocephalus* sp., which cannot be allocated to a particular host group) in 3 of 103 individual coho from Parvin Lake, and none from Granby Reservoir, Colorado. Both bodies of water have a fairly large number of species of salmonid fishes (mostly introduced), but only in Parvin Lake did salmonid fishes, mainly rainbow trout and splake (*Salvelinus fontinalis* X *S. namaycush* hybrid), dominate the community.

Becker and Brunson (1968) reported plerocercoids of *Proteocephalus ambloplitis* in 9 of 243 young coho, but none of 20 two-year old coho planted in Goodwin Lake, Washington, which has a resident population of largemouth bass, *Micropterus salmoides*. They did not mention any other parasites.

Kokanee were introduced into Lake Huron, which has a predominantly non-salmonid fish community (Bangham, 1955; Collins and Dechtiar, 1974). A large proportion of non-salmonid fishes were gill-netted along with the introduced kokanee, suggesting a close association (Collins and Dechtiar, 1974). Only 8 out of 18 parasite species recovered from the kokanee were salmonid fish parasites. However, a large proportion were infected with infected with *M. salmonis*, *Echinorhynchus leidyi* and *C. stigmatura*, all of which were commonly found in salmonid fishes.

Wootten (1973) examined rainbow trout and brown trout introduced as adults into Henningfield Reservoir, Essex, which had no salmonid fish. They harboured 11 and 13 parasite species respectively, including

D. sagittata and *Eubothrium crassum*, salmonid parasites which were probably introduced with the trout. Most of the parasites acquired were ectoparasites or larval parasites which culminated their life cycle in piscivorous birds. Very few endoparasites were acquired.

Some of the parasites acquired by coho are known to be pathogenic to other hosts. Heavy infections of *E. salvelini* apparently have no effect on lake trout, but small numbers of young tapeworms were found to have detrimental effects on growth and swimming performance in infected juvenile sockeye salmon (*O. nerka*), which resulted in an increased susceptibility to predators (Smith, 1973). The parasite is primarily one of fry or smolt in sockeye salmon (Boyce, 1974; Smith, 1973), and Boyce showed that susceptibility to infection decreased rapidly as the young salmon grew. No evidence of damage was found in the few coho infected with *Eubothrium* plerocercoids. The coho may have already grown past the stage most susceptible to infection when introduced.

In brown trout infected with *C. truncatus*, the mucosal layer of infected pyloric caeca was destroyed, with fibrous tissues formed at the site of attachment; in older infections, this reaction caused the fusion of neighbouring pyloric caeca (Awachie, 1966; Halvorsen and Macdonald, 1972). Such thickened fibrous tissues were observed in heavily infected whitefish, but few coho were infected with *C. truncatus* and no observations were made on the possible effects on the new host.

Infection of *Ergasilus* on the gill filaments may cause a strong reaction from the host, resulting in the destruction of the gill epithelium and a fusion of gill lamellae (Bauer, 1959; Kabata, 1970; Rogers, 1969). Einszporn-Orecka (1970) showed that *Tinca tinca* infected with *E. sieboldi* had a general low blood protein and a decrease in

erythrocytes which could cause anaemia. He considered that heavy infections with *E. sieboldi* could cause the death of fishes.

No visible reaction was observed in coho heavily infected with *E. auritus* and *E. nerkae*. However, no histological examination of the infected regions were made.

Simon and Simon (1936) observed some pathological changes, particularly in the gonads, in mountain whitefish, eastern brown trout and rainbow trout infected with *P. agubernaculum*. In heavily infected coho, large numbers of *P. agubernaculum* were found between the pyloric caeca and were accompanied by thread-like adhesions between adjacent pyloric caeca or to the coelomic wall.

Although no histological sections of intestines heavily infected with *M. salmonis* were examined, there was an obvious tissue thickening at the site of proboscis attachment in the posterior region of heavily infected whitefish. The heavy infection of *M. salmonis* in coho might cause some host reaction.

In view of the fact that infections of *E. salvelini*, *C. truncatus*, *P. agubernaculum*, *M. salmonis*, *E. auritus* and *E. nerkae* do cause pathological reactions in other hosts, these same species, particularly the last four which infected coho heavily (at least in some years), could have had some detrimental effects on the introduced coho. The lack of success of the introduction of coho into Cold Lake might have been due in part to the heavy infections with these parasites.

VII. THE BIOLOGY OF *METECHINORHYNCHUS SALMONIS*

It is obvious that the patterns in the parasite communities were set by the dominant parasites, essentially those of salmonid fishes, and particularly *M. salmonis*, the most dominant parasite. Since *M. salmonis* exerted such a strong influence on the parasite communities, it deserves special attention; its biology is examined in greater detail in this section.

At least some individuals of each species of fish examined in the present study were infected, with high prevalences in whitefish, lake trout, coho, longnose sucker, pike and burbot; stickleback and white-sucker had the lowest prevalence (Table 21). Lake trout (with a mean intensity of 421) and three-year old coho (533), two predators, had very high mean numbers of individuals; ninespine sticklebacks had the least (1.8).

Female *M. salmonis* were arbitrarily assigned to one of three stages of maturation as described by Tedla and Fernando (1970): 1) females with ovarian balls predominant; 2) females with non-shelled acanthors predominant; and 3) females with shelled acanthors predominant (gravid) in the body cavity. Unfixed female acanthocephalans were teased apart and their maturation assessed under a compound microscope. The maturation of preserved acanthocephalans was assessed after dehydration in glacial acetic acid and clearing in creosote (Chubb, 1962).

Gravid females comprised a large proportion (about 50%) of the *M. salmonis* in both cisco and 3-year old coho, a moderate proportion

Table 21. Prevalence, mean intensity, number of females and maturation of *Metechinorhynchus salmonis* in various host species in Cold Lake

	No. exam.	Prevalence	Mean intensity ± S.E.	Total no. female acanthocephalans	% female gravid acantho-cephalans
Lake whitefish	836	99.5	170.2 ±5.8	31585	14.2
Cisco	(961)[3]	32.4	8.7 ±0.7	3127	49.6
Lake trout	35	100	420.9 ±39.2	3847	24.3
Coho salmon (II)[1]	210	99.0	57.5 ±5.4	980	20.4
Coho salmon (III)[2]	78	100	532.9 ±43.2	18525	56.9
Walleye	12	66.7	3.0 ±0.4	19	0
Ninespine sticklebacks	1038	19.0	1.8 ±0.1	50	0
Whitesucker	36	8.3	4.0 ±3.0	4	0
Longnose sucker	12	83.3	30.9 ±5.8	77	0
Northern pike	62	83.9	30.6 ±5.8	72	2.8
Burbot	29	100	174.4 ±23.8	1003	1.7

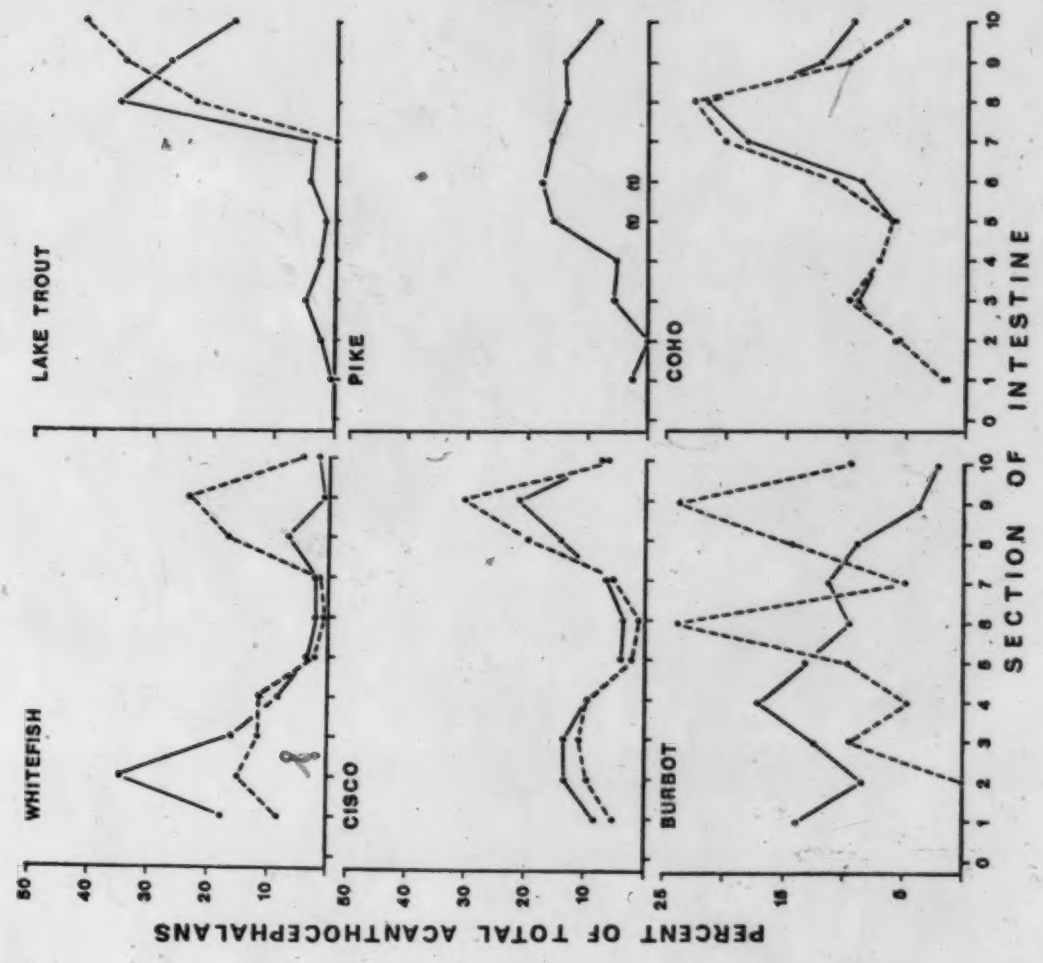
[1]fish introduced in spring and recaptured through fall.
[2]fish overwintered in the lake.
[3]757 + 204 examined only for *M. salmonis*.

(10-25%) in other salmonids, and a very small proportion (less than 3%) in pike and burbot (Table 21). The majority of the worms in pike and burbot, and all of those recovered from walleye, stickleback, whitesucker and longnose sucker showed some growth, but otherwise little change from excysted cystacanths.

The distribution of *M. salmonis* within the gut of the fish was examined in all fish taken after May, 1973. At necropsy, the intestine was divided into ten sections of equal length, and the number of parasites in each section was determined.

The distributions of *M. salmonis* in the fishes examined are shown in Figure 18. In whitefish, the acanthocephalans were concentrated at the anterior end, where they were found mainly in the pyloric caeca. However, a higher proportion of those in the posterior end were gravid females, so that almost equal proportions of the gravid females were found in the anterior and posterior regions. In cisco, approximately equal numbers of acanthocephalans were found in the anterior (pyloric caeca) and posterior regions, but the gravid females were predominately in the posterior region. In lake trout, the acanthocephalans, and particularly the gravid females, were virtually limited to the posterior third of the intestine. In coho, the acanthocephalans, including the gravid females, were found throughout the intestine, but peak numbers were in the posterior region. In pike, the acanthocephalans were distributed fairly evenly throughout the posterior half of the intestine, but both the two gravid females were found in the mid-intestine. In burbot, they were widely dispersed, with most of the worms in the anterior half of the intestine, although most of the gravid females were in the posterior half.

Figure 18. Intra-intestinal distribution of *Metechinorhynchus salmonis* (as percentage of total number (————)) and gravid female *M. salmonis* (as percentage of total number (--------)) in fishes from Cold Lake, Alberta


WHITEFISH
CISCO
BURBOT
LAKE TROUT
PIKE
COHO
PERCENT OF TOTAL ACANTHOCEPHALANS
SECTION OF INTESTINE

The mean intensity of *M. salmonis* increased considerably, and in a linear fashion, with age in whitefish (Figure 19). Consequently, their maturation and distribution in this species of host were analyzed by age class. The proportion of gravid females reached a peak in age class IV, then declined through age class VIII (Figure 19). Despite the tremendous increase in mean intensity between age classes IV and IX, there was no significant variation in the mean intensity of gravid females among these age classes (overall mean, 11 ± 0.74).

The intraintestinal distribution of the *M. salmonis* changed with age, gradually shifting from a pattern with a high peak at the posterior region of the gut (essentially similar to the pattern in cisco) in young whitefish to one with a high peak in the anterior region of the intestine in the old whitefish (Figure 20). Although the proportion of the acanthocephalans in the posterior 30% of the intestine declined with age, the mean number of acanthocephalans in that portion of the intestine did not vary significantly in age classes IV through IX. The shift in distribution was due to the establishment of additional acanthocephalans in the anterior part of the intestine, and suggested that availability of space, particularly the size of the opening and the length of the pyloric caeca, was important for attachment.

The patterns of distribution of gravid female *M. salmonis* were similar to those of the total acanthocephalans, with a high peak at the posterior region of the intestine in young whitefish and a high peak at the anterior region of the intestine in old whitefish (Figure 21). The mean numbers of gravid female acanthocephalans in the last 30% of the intestine did not vary significantly in age classes IV through IX, but the number in the anterior 30% did increase significantly. These

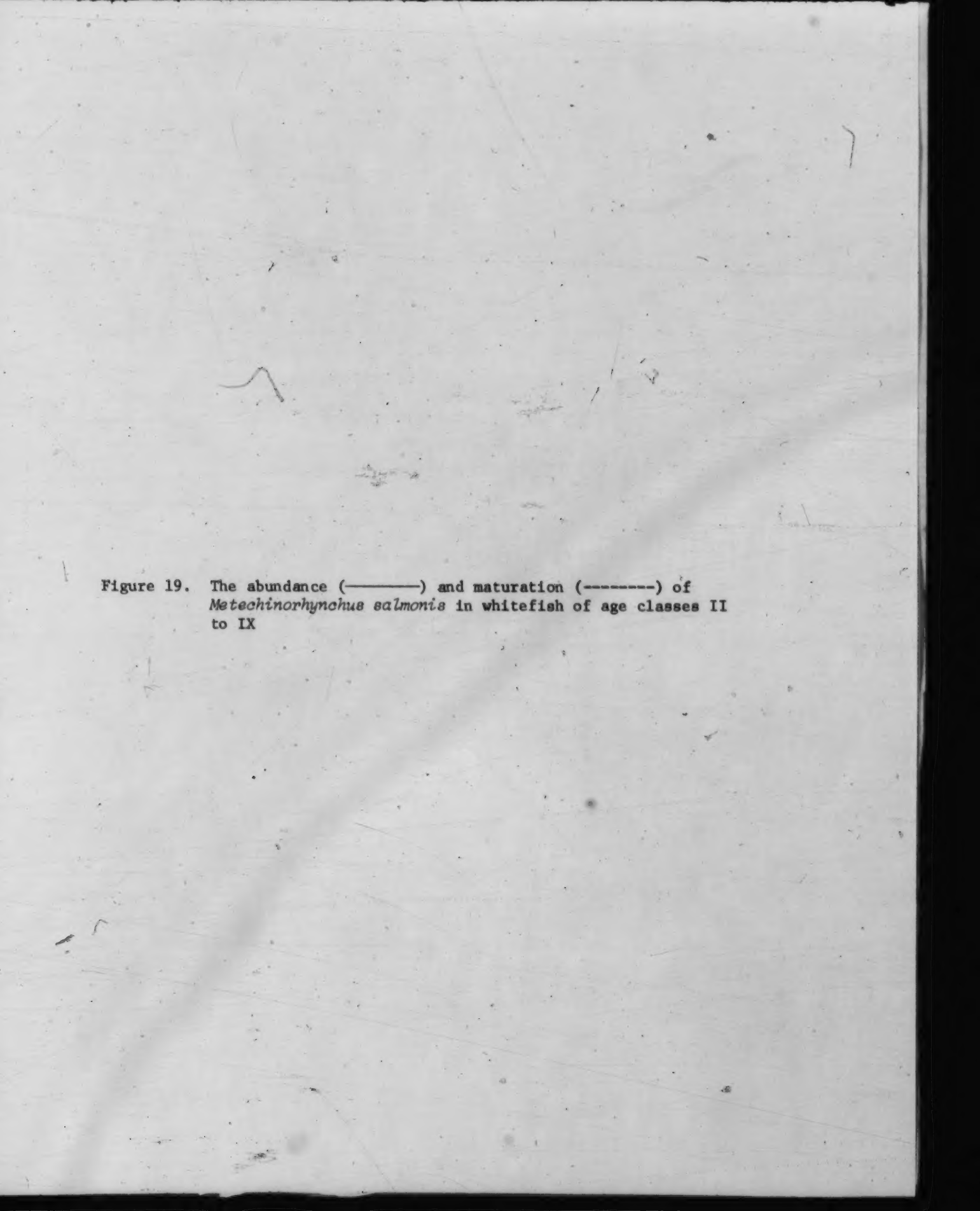


Figure 19. The abundance (————) and maturation (--------) of *Metechinorhynchus salmonis* in whitefish of age classes II to IX

PERCENT OF GRAVID FEMALES
16
12
8
4
MEAN INTENSITY
250
200
150
100
50
II
III
IV
V
VI
VII
VIII
IX
AGE

Figure 20. Distribution of *Metechinorhynchus salmonis* in the intestine of lake whitefish of age classes II, IV, VI and IX

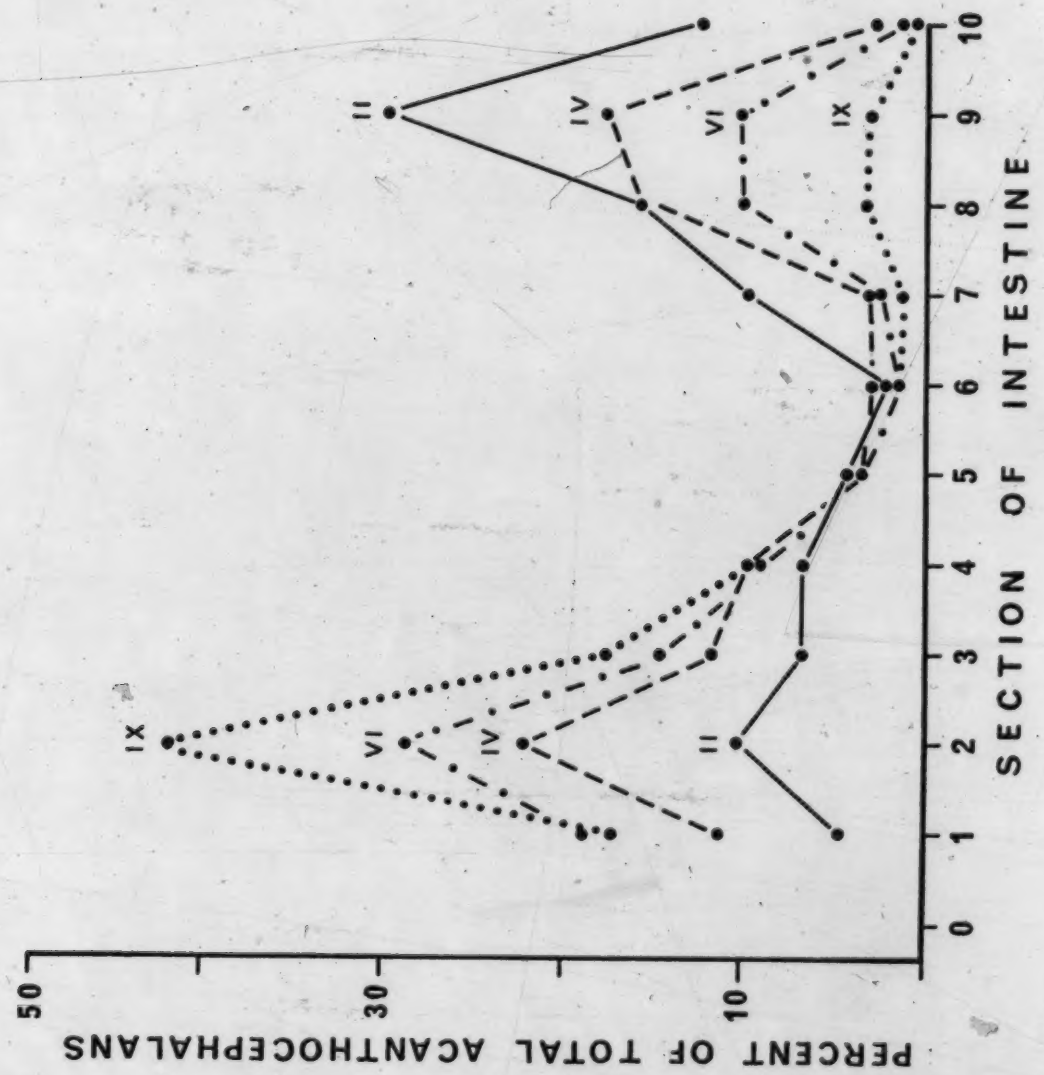
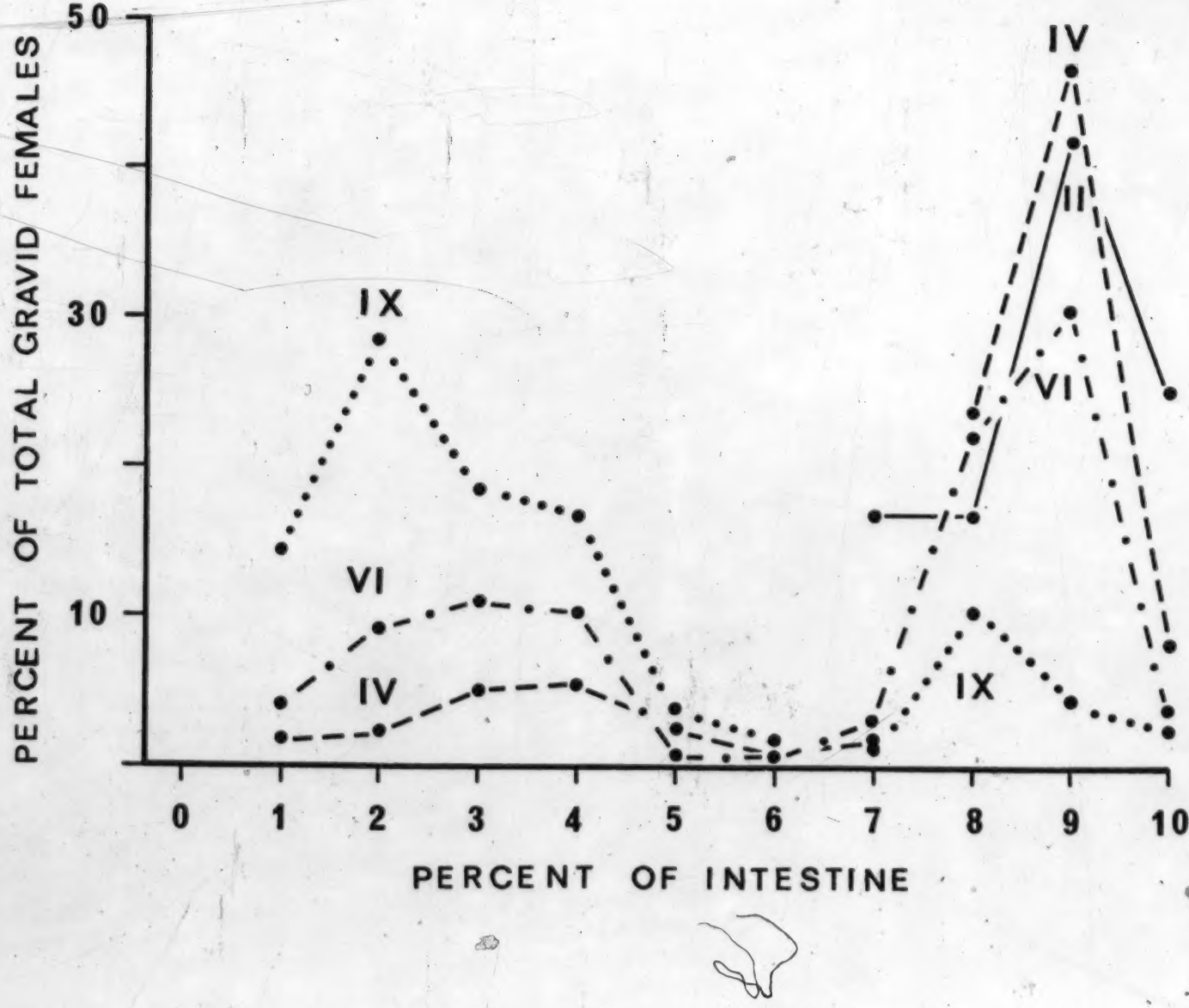

PERCENT OF TOTAL ACANTHOCEPHALANS
50
30
10
0
1
2
3
4
5
6
7
8
9
10
SECTION OF INTESTINE
II
IV
VI
IX
XI

Figure 21. Distribution of gravid female *Metechinorhynchus salmonis* in the intestine of lake whitefish of age classes II, IV, VI and IX


PERCENT OF TOTAL GRAVID FEMALES
50
30
10
IX
VI
IV
IV
II
VI
IX
0
1
2
3
4
5
6
7
8
9
10
PERCENT OF INTESTINE

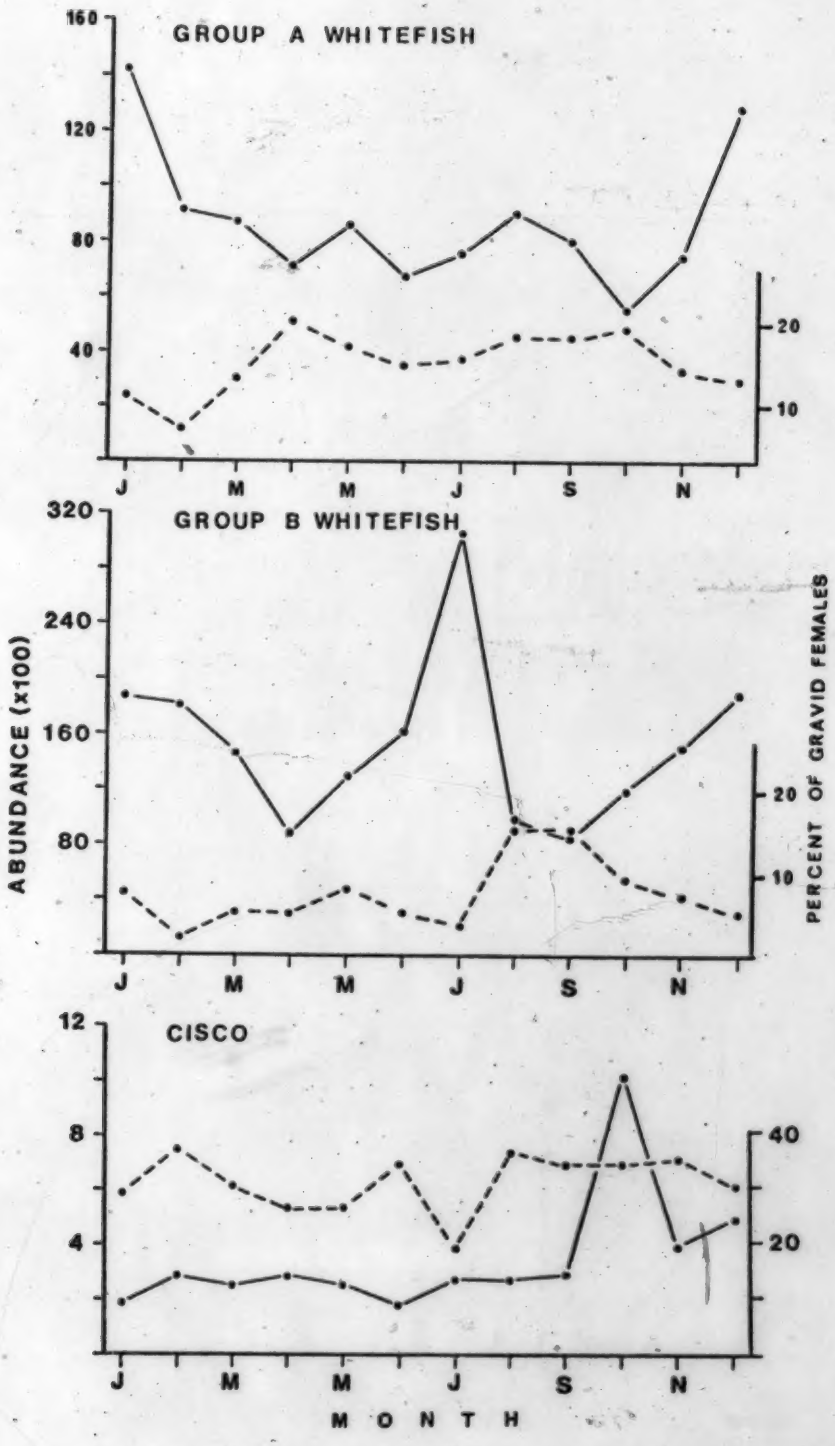
observations suggested that the acanthocephalans did not move down the intestine for maturation, as suggested earlier by Awachie (1966a) and Tedla and Fernando (1970).

The seasonal patterns of abundance of *M. salmonis* have been presented earlier. In brief, peak abundances were reached in early winter in both groups of whitefish and in cisco. Group B whitefish showed a second, late summer, peak, which was less obvious in the Group A whitefish and absent in cisco.

Gravid female *M. salmonis* were found in the intestine throughout the year. In whitefish, there was no obvious seasonal pattern in the proportion of gravid females in the population (Figure 22); rather, the percent gravid females showed a general inverse relationship to the total number of acanthocephalans in the same samples (Group A whitefish: $r = -0.55$, $t = 2.06$, $P < 0.1$; Group B whitefish: $r = -0.64$, $t = 2.64$, $P < 0.05$). The numbers of gravid females did not vary significantly among months. In cisco, neither the percentage of gravid females nor the number of gravid females varied significantly among months.

The preceding analyses suggest that the maturation of female *M. salmonis* is affected by the number of acanthocephalans present and the age (or, more probably, the size) of the fish, and that the effects of these factors differ among species of hosts. The lower percentages of gravid females in whitefish and trout, which also harboured significant numbers of mature cestodes, than in cisco and coho, which had few (or small, immature) cestodes, suggest that the number of cestodes also may be affecting maturation. Consequently, data on individual fish of each of these four species of salmonids were examined to determine the relationships between maturation of *M. salmonis* (measured by the number of gravid

Figure 22. Seasonal patterns in the abundance (————) and maturation (--------) of *Metechinorhynchus salmonis* in whitefish and cisco


GROUP A WHITEFISH
160
120
80
40
20
10
J
M
M
J
S
N
GROUP B WHITEFISH
320
240
160
80
20
10
ABUNDANCE (x100)
PERCENT OF GRAVID FEMALES
J
M
M
J
S
N
CISCO
12
8
4
40
20
J
M
M
J
S
N
M O N T H

females (G) and by the percentage of gravid females (PG)) and the total number of acanthocephalans (A), the number of cestodes (C), and the size of the host (measured by fork length (FL) in trout, by the length of intestine (IL) in the others).

In whitefish, all variables were significantly interrelated (Table 22). The number of gravid females (G_w) was positively related to all three independent variables. However, the stepwise multiple regression analysis indicated that the number of acanthocephalans was the most important independent variable, that the length of intestine also explained a significant amount of the variance, but that the number of cestodes did not (Table 23). The multiple regression equation is:

$$G_w = 0.015 + 0.035A_w + 0.031IL_w$$

which accounted for 11.2% of the variance ($P < 0.001$).

The percent of gravid females in whitefish (PG_w) was negatively related to the other variables (Table 22), but only the number of acanthocephalans explained a significant amount of the variance (Table 23). The regression equation is:

$$PG_w = 15.71 - 0.027A_w$$

and accounted for only 6.1% of the variance ($P < 0.001$).

In cisco, there were no significant relationships between the number of acanthocephalans, the number of cestodes, and the length of the intestine. The number of gravid females (G_c) was positively related to the independent variables A_c and IL_c (Table 22) and the stepwise multiple regression analysis indicated that each explained a significant amount of variance (Table 23). The number of acanthocephalans was an extremely

Table 22. Correlation coefficients between variables; values above the diagonal are for numbers of gravid females, those below the diagonal for percent of gravid females. The symbols are explained in the text

	Whitefish (n=379) PG	A	C	IL	Cisco (n=396) PG	A	C	IL
G	—	0.32**	0.12*	0.24**	—	0.86**	-0.05	0.13**
A	-0.25**	—	0.59**	0.47**	-0.01	—	-0.01	0.07
C	-0.16**	0.59**	—	0.24**	-0.10*	-0.01	—	-0.02
IL	-0.10*	0.47**	0.24**	—	0.15***	0.07	-0.02	—

	Trout (n=11) PG	A	C	FL
G	—	0.54	0.19	0.48
A	-0.25	—	0.37	0.63
C	-0.35	0.37	—	0.02
FL	0.18	0.63	0.02	—

	Coho (n=36) PG	A	IL
G	—	0.84**	0.09
A	-0.04	—	0.35*
IL	-0.27	0.35*	—

* P<0.05
** P<0.001

Table 23. The percent of the variance in the number of gravid females and the percentage of gravid females which are explained by the independent variables in the stepwise multiple regression

Variable	Whitefish	Cisco	Trout	Coho
Number of gravid females(G)				
A	10.0***	73.1***	29.0	69.2***
C	0.6	0.2	0	N/A
IL/FL	1.2*	0.5**	0.3	4.4**
Percent of gravid females(PG)				
A	6.1***	0	11.8	7.5
C	0	0.9+	12.1	N/A
IL/FL	0	2.3***	3.4	0.3

\+ P<0.10
* P<0.05
** P<0.01
*** P<0.001

important independent variable, explaining almost three-fourths of the variance. The multiple regression equation is:

$$G_C = -3.643 + 0.311A_C + 0.035IL_C$$

which accounted for 73.6% of the variance ($P < 0.001$).

The percent of gravid females in cisco (PG_C) was significantly negatively related to the number of cestodes and significantly positively related to the length of the intestine (Table 22). The length of intestine explained a significant amount of variance and the variance explained by the number of cestodes was of borderline significance ($P < 0.1$). The regression equation is:

$$PG_C = -1.396 + 0.432IL_C - 0.318C_C$$

but it accounted for only 2.3% of the variance ($P < 0.001$).

In lake trout, the correlation coefficients between each pair of variables (except C and FL) were relatively high, but not statistically significant, probably due to the very small sample size (Table 22). The number of gravid females (G_T) was positively related to all three independent variables. The stepwise multiple regression analysis indicated that the number of acanthocephalans was the most important independent variable, though not statistically significant, and that the other variables were of little importance (Table 23). The regression equation is:

$$G_T = 38.55 + 0.058A_T$$

which accounted for 29% of the variance ($P < 0.1$).

The percent of gravid females in trout (PG_T) was negatively related to the numbers of acanthocephalans and of cestodes, but positively related to the size of the fish (Table 22). Each variable explained a proportion of the variance greater than proportions that were significant in other analyses, but, probably because of the small sample size, none were statistically significant (Table 23). The regression equation is:

$$PG_T = -6.353 - 0.075C_T + 0.06FL_T - 0.02A_T;$$

it accounted for 27.3% of the variance, but was not statistically significant ($P > 0.1$).

In coho, the number of cestodes was very small, so that variable was not included in this analysis. The number of gravid females was positively related to the total number of acanthocephalans, which was positively related to the length of intestine (Table 22). The stepwise multiple regression analysis indicated that the number of acanthocephalans was the most important independent variable, explaining over two-thirds of the variance, and that the length of intestine also explained a significant amount of the variance, but was negatively related to the number of gravid females (Table 23). The multiple regression equation is:

$$G_s = 14.99 + 0.432A_s - 0.747IL_s$$

and accounted for 73.6% of the variance ($P < 0.001$).

The percent of gravid females in coho (PG_s) was not significantly related to the other variables (Table 22). Neither the number of acanthocephalans nor the length of intestine explained a significant

amount of the variance. Together, they only accounted for 7.8% of the variance ($P > 0.1$).

DISCUSSION

There are several apparent reasons for the dominant position of *M. salmonis* in the Cold Lake ecosystem. First, *M. salmonis* is a parasite of the salmonids, which dominate the community of fishes. As pointed out earlier, the parasites of salmonids generally dominated the community of parasites.

Second, individual species of acanthocephalans of fish are frequently found in a wide variety of fish (Hoffman, 1967; Petrochenko, 1971). *Metechinorhynchus salmonis* is no exception to this wide host specificity; in the present study, all 10 species of fishes were infected.

Third, there are alternate ways of reaching the fish hosts. The basic life cycle of *M. salmonis* is through *P. affinis*, the intermediate host. The amphipod formed a major part of the diet of whitefish and burbot; in each, the acanthocephalans dominated the parasite community. Amphipods (in Cold Lake, probably *P. affinis*, as deduced from the heavy infections with *M. salmonis*) formed a significant portion of the diet in longnose suckers (Scott and Crossman, 1973), and lesser portions of the diets of cisco and probably of whitesuckers and sticklebacks.

However, the large numbers of *M. salmonis* in trout and coho, which eat few, if any, *P. affinis*, suggest a second route of infection, using sticklebacks, cisco and probably young whitefish as transport hosts. The use of such transport hosts is well established for other

acanthocephalans of fish (Petrochenko, 1971). Cisco and particularly sticklebacks formed significant portions of the diets of the predatory fishes in Cold Lake.

Although all fish species examined were found infected with *M. salmonis*, gravid female acanthocephalans were found only in salmonid fishes: whitefish, cisco, trout and coho. The small number of gravid females in pike and burbot might be due to a direct transfer from feeding on infected cisco, since Hnath (1969) has shown that mature *M. salmonis* from coho could survive, for up to 12 weeks, when transferred to brook trout.

To illustrate the relative importance of the alternate life cycle pathways, and the relative importances of the various definitive hosts, I have devised a model of the circulation of *M. salmonis* in the community of fishes in Cold Lake (Figure 23). It must be emphasized that flow rates were not measured in this study. Instead, they were deduced from a static picture of the distribution of *M. salmonis* in the various species of fishes.

The model is based on data on the abundance (prevalence times mean intensity) and percent of gravid females in each of the ten species of fishes examined. The figure for the abundance in each host species was multiplied by the weighting factor (see p. 16 for assumptions implicit in the derivation of that factor) to account for the relative population size of that host, then divided by the sum of the products for all ten fishes to give a first approximation of the proportion of the *M. salmonis* population in that host species (PP_1 in Table 24).

In previous sections, I have shown that populations of *M. salmonis* in whitefish and cisco vary significantly with season and age.

Figure 23. The relative flow rates of *Metechinorhynchus salmonis* in a community of fishes in Cold Lake, Alberta. The solid arrows indicate flow from the intermediate host, *P. affinis*, to various fishes, either directly or through transport hosts (arrows leading from ninespine sticklebacks and cisco). The double arrows indicate flow of eggs from definitive hosts to the intermediate host. Values on the arrows indicate the proportional value of that flow. Values under each fish host are the proportion of the population of *M. salmonis* in that host, followed by percentage of gravid females. See text for detailed explanation.

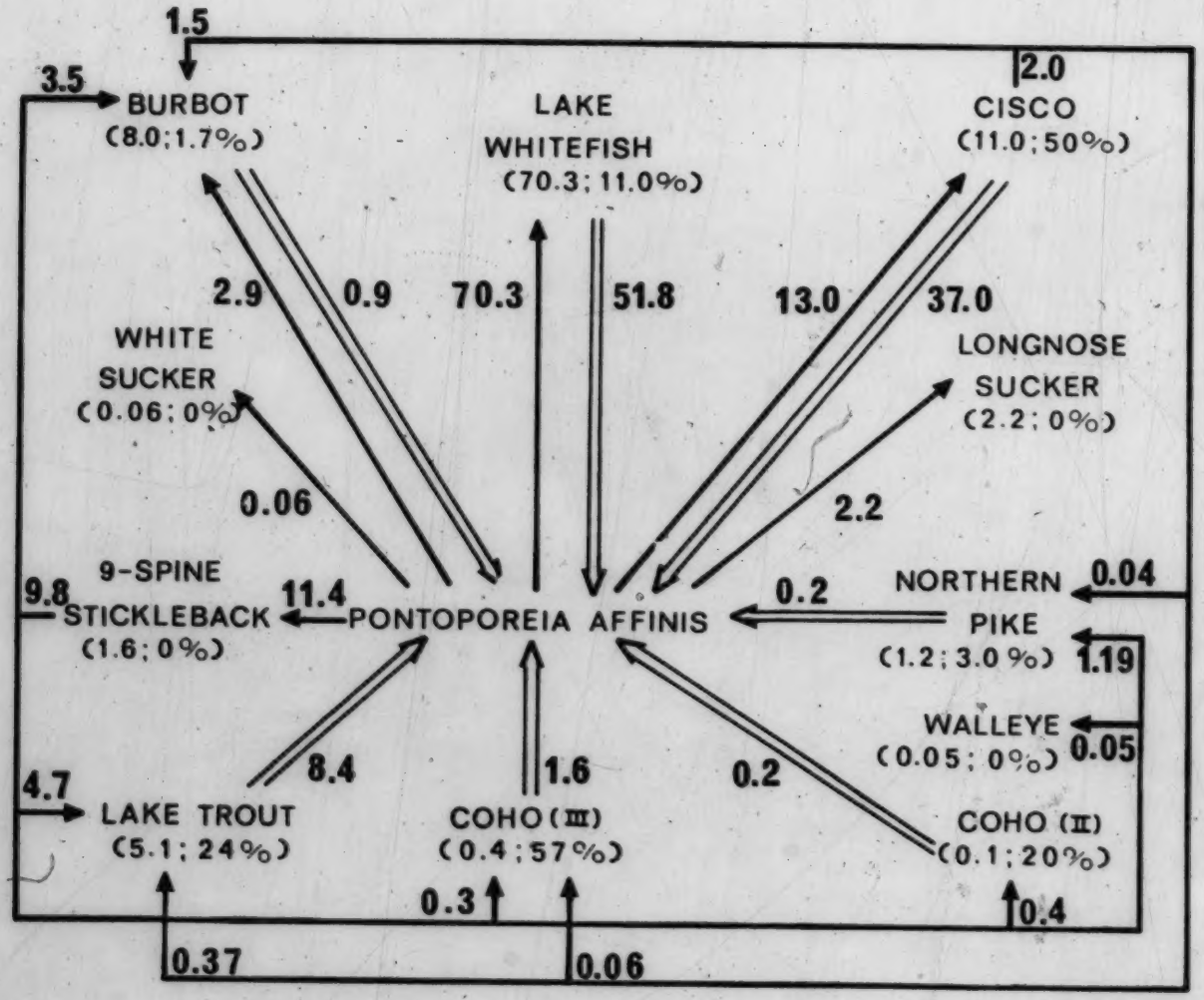

1.5
3.5
BURBOT
(8.0;1.7%)
LAKE
WHITEFISH
(70.3;11.0%)
2.0
CISCO
(11.0;50%)
2.9
0.9
70.3
51.8
13.0
37.0
WHITE
SUCKER
(0.06;0%)
LONGNOSE
SUCKER
(2.2;0%)
0.06
2.2
9-SPINE
STICKLEBACK
(1.6;0%)
9.8
11.4
PONTOPOREIA AFFINIS
0.2
NORTHERN
PIKE
(1.2;3.0%)
0.04
1.19
WALLEYE
(0.05;0%)
0.05
4.7
8.4
1.6
0.2
LAKE TROUT
(5.1;24%)
COHO (III)
(0.4;57%)
COHO (II)
(0.1;20%)
0.3
0.4
0.37
0.06

Table 24. The proportion of acanthocephalan populations, percent gravid females and proportion of output of eggs in various species of fish, Cold Lake, Alberta

	Abundance	Weighting factor	Unadj. PP_1*	Adjusted for age, season PP_2	PP_3	PP_4	Unadj. PM_1**	Adjusted for age, season PM_2	PM_3	PM_4	Unadj. PE_1***	Adjusted for age, season PE_2	PE_3	PE_4
Whitefish	16934.9	28.5	90.2	74.6	70.3	62.8	14.2	11.2	11	10.7	80.9	56.2	51.8	44.6
Ciaco	281.9	100	5.3	10.3	11.0	12.3	50	50	50	50	16.9	34.6	37.0	40.6
Lake Trout	42090	0.16	1.3	4.2	5.1	6.9	24				1.9	6.8	8.4	11.1
Coho (II)	5712.3	0.03	0.03	0.1	0.1	0.2	20				0.04	0.2	0.2	0.2
Coho (III)	53290	0.01	0.1	0.3	0.4	0.5	57				0.4	1.3	1.6	2.1
Pike	2567.3	0.6	0.3	1.0	1.2	1.6	3.0				0.05	0.2	0.2	0.3
Whitesucker	33.2	2.18	0.01	0.05	0.06	0.07	0				0	0	0	0
Longnose Sucker	2574	1.1	0.5	1.8	2.2	2.9	0				0	0	0	0
Burbot	17440	0.6	2.0	6.5	8.0	10.7	1.7				0.2	0.7	0.9	1.2
Stickleback	34.2	60	0.4	1.3	1.6	2.1	0				0	0	0	0
Walleye	200.1	0.3	0.01	0.04	0.05	0.06	0				0	0	0	0

* Proportional acanthocephalan population
** Percent gravid female
*** Percent of eggs produced
Subscripts indicate: 1 - unadjusted; 2 - mortality rate at 50%; 3 - mortality rate at 61%; 4 - mortality rate at 72%.

Abundances in these hosts were therefore corrected to account for this variance. The derivation of a seasonal correction factor will be illustrated for Group A whitefish. Since this group contained two age classes, collected in different numbers, I corrected for age effects within this group by calculating a weighted mean (abundance in age IV times the number of age IV fish examined, plus abundance in age V times the number of age V fish, divided by the total of age IV and V fish). The mean of the monthly abundances was divided by this weighted mean to give a correction factor of 0.94, which was used to adjust the abundances (from Appendix IV) of all immature whitefish (age classes II-VI). Similarly, a correction factor calculated for Group B whitefish (1.07) was used to adjust the abundances of mature whitefish (age classes VII-X). A single correction factor (1.12) was calculated and used (on data in Appendix VI) for cisco.

Correction for seasonal variation in abundance of *M. salmonis* in coho was difficult. Coho grew rapidly, and acquired increasing populations of *M. salmonis*, during the summer. My collections were biased towards these larger fish. The uncorrected mean overestimated the abundance of *M. salmonis* in young coho during the summer, but underestimated the abundance during the fall and winter. Since there was no evidence in my data of a seasonal "spawning period" such as that shown for *M. salmonis* in Lake Ontario by Tedla and Fernando (1970), I assume that:

1. Transmission of *M. salmonis* to *P. affinis* may occur throughout the year.

The uncorrected abundance for coho would therefore be as good as any other estimate.

In order to correct for the variation due to age, two factors had to be taken into account, the abundance of *M. salmonis* in each age class, and the relative abundance of host fish in each age class. Seasonally corrected values determined above were used for the former. The latter was calculated by applying an estimate of the annual mortality rate to a hypothetical cohort of 100 class II whitefish (or class I cisco), then calculating the proportions of each age class in the total population.

The mortality rate in Cold Lake was estimated by the differences in total numbers of fish examined in age classes VIII (240), IX (130), and X (19). The reduction between age classes VIII and IX suggested a mortality rate of approximately 50%, the reduction between IX and X a rate of approximately 72%, and that between VIII and X a rate of approximately 61%. The last was very close to the mortality rate estimated by Kennedy (1953) for whitefish in Great Slave Lake, N.W.T., and has been used in the model. A similar mortality rate was assumed for cisco.

The corrected abundance of *M. salmonis* in whitefish (or cisco) was the sum of the products of the seasonally adjusted abundance in each age class multiplied by the proportion of the fish in that age class. These values were used to recalculate the proportion of the *M. salmonis* in each host species (PP_3 in Table 24 and the first value in parenthesis in Figure 23). Proportional populations of *M. salmonis* calculated using the other mortality rates are shown in Table 24.

The input of *M. salmonis* to each host species was initially considered to be equivalent to the proportional population in that species. This assumes that:

2. A *M. salmonis* ingested by any host has the same probability of becoming established, and therefore, that
3. The rate of ingestion of *M. salmonis* by each host species is proportional to the population in that host.

Since there are alternate ways of reaching the fish hosts, the input to each host species had to be apportioned to each of these ways, according to the food habits of the host species. Whitefish, cisco, both species of suckers and sticklebacks did not feed on fish (the small numbers taken by whitefish or cisco are negligible), therefore all input to these species was assumed to be directly from *P. affinis*. Walleye fed only on sticklebacks; all input to walleye was assumed to be by this route. Lake trout and pike did not feed on *P. affinis*, and coho fed on them to a negligible extent, but all fed on both cisco and sticklebacks; the input to each was apportioned to each transport host in proportion to the total number of each forage fish eaten by the predators examined times the abundance of *M. salmonis* in that species of forage fish. This assumes that:

4. The probability of becoming established is the same for a *M. salmonis* ingested in *P. affinis* or in a transport host.

Burbot fed on *P. affinis* and on both transport hosts: *P. affinis* made up 37.5% of the total occurrences of *P. affinis* and fish in the diet, therefore 37.5% of the input of *M. salmonis* to burbot was assumed to be through the amphipod. The remainder of the input was apportioned as above. The input of *M. salmonis* to various predators calculated using the other mortality rates is shown in Table 25.

For each of the two transport hosts, the inputs through that

Table 25. The relative flow rates of *Metechinorhynchus salmonis* by alternate routes to various predators

	Unadjusted	Adjusted survival rate of		
		.5	.39	.28
Trout	RF_1	RF_2	RF_3	RF_4
Sticklebacks	1.2	3.89	4.73	6.4
Cisco	0.09	0.31	0.37	0.5
Pike				
Sticklebacks	0.296	0.988	1.186	1.58
Cisco	0.0035	0.019	0.044	0.02
Burbot				
Sticklebacks	0.87	2.84	3.5	4.68
Cisco	0.376	1.22	1.5	2.01
Pontoporeia	0.75	2.44	3.0	4.01
Coho (II)				
Sticklebacks	0.030	0.1	0.13	0.2
Coho (III)				
Sticklebacks	0.084	0.253	0.337	0.422
Cisco	0.0157	0.017	0.0627	0.0784

transport host to all predators were summed and added to the input to that transport host from *P. affinis*. The resultant proportional flow rates are shown on the arrows leading away from *P. affinis* in Figure 23.

The relative number of gravid *M. salmonis* from each host species was calculated as the abundance of *M. salmonis* times the proportion of gravid females in that host species (the second value in parentheses in Figure 23) times the weighting factor for the population of that host species. (The proportions of gravid females in whitefish and cisco were corrected for age and season using the procedures described above.) This value, divided by the sum of the values for all host species, was considered to be the relative output from that host species. These values are shown on the wide arrows leading to *P. affinis* in Figure 23. This calculation of output assumes that:

5. The turnover rate for gravid female *M. salmonis* is the same in all definitive host species;
6. The number of eggs per gravid female is the same in all definitive host species; and that
7. The probability of infecting *P. affinis* is the same for an egg from a gravid female from all definitive host species.

The model (Figure 23) shows that the majority of *M. salmonis* within the ecosystem flow through the basic life cycle from *P. affinis* to whitefish and back to *P. affinis*. A second major component is from *P. affinis* to cisco and back. Only about one-eighth of the flow was through transport hosts, primarily sticklebacks.

The output values in Figure 23 suggest that there are only three significant definitive hosts for *M. salmonis* in Cold Lake: whitefish,

cisco and trout. Despite large populations of *M. salmonis* in individual coho, and a high proportion of gravid females, the relative abundance of coho is so low that acanthocephalans in this host account for only a small proportion of the output. Burbot and pike were relatively abundant (more so than lake trout or coho), and both contain higher populations of *M. salmonis* per infected fish than cisco, but the low proportions of gravid females make the output from these host species negligible.

The populations of *M. salmonis* in each of the three significant definitive hosts appear to be controlled in different ways. In whitefish, the primary control appeared to be through a density-dependent regulation of the number of gravid females. There are three lines of evidence for this. First, the fairly constant mean number of gravid females in fish of age classes IV through IX, despite the tremendous increase in total numbers with age. Second, the fairly constant mean number of gravid females throughout the year, despite significant seasonal variation in total numbers. Third, and most instructive, the significant negative regression of percent gravid females on total numbers of acanthocephalans in individual fish. As a result of this control on maturation, the proportional output from whitefish was considerably less than the proportional input to whitefish. This type of negative feedback is an example of Bradley's (1972) Type III regulation (through the host individual), but operating on the output, rather than the "infra-population" (using the terminology of Esch *et al.*, 1975). This type of control is well-known in nematodes; for example, Michel (1970) showed that in equilibrium populations fifth-stage larvae of *Ostertagia ostertagi* could mature only when adults died.

In lake trout, the mean number of acanthocephalans and the mean number of gravid females were much higher than in whitefish, but the proportion of gravid females was much lower than in cisco or coho. The lake trout also harboured large numbers of *E. salvelini*. The multiple regression analysis showed the number of cestodes to be the most important variable determining the percent gravid females, explaining a substantial proportion (12%) of the variance (although, probably because of the small sample size, this proportion was not statistically significant). In this species of host, therefore, the regulation of maturation, and hence of output, appears to be a function of inter-specific interaction.

In contrast, there appeared to be no negative feedback system operating in cisco. Populations of *M. salmonis* in this host were low (mean of 8.7 per infected fish), but there was a high proportion (50%) of gravid females. Cisco appeared to acquire *M. salmonis* entirely through their relatively infrequent feeding on *P. affinis*. This appears to be an example of Bradley's (1972) Type I regulation (through transmission).

No negative feedback system appeared to be operating in coho, either, but in this host, populations of *M. salmonis* were very high, with a high proportion (57%) of gravid females. Perhaps this indicates that no regulation of population has been developed in this new host-parasite system.

The question arises: In which host does the regulation of the acanthocephalan population in the whole ecosystem take place? It might be in the intermediate host; I have no data on that part of the system. However, the model shows that most of the acanthocephalans in the

ecosystem flow through whitefish. Using different mortality rates, this value varies between 2/3 and 3/4 of all acanthocephalans (Table 24). This high flow through the whitefish appears to be due to two factors, the abundance of whitefish in the lake, and the high proportion of *P. affinis* in their diet. The negative feedback operating through control of the rate of maturation of females reduces the output of eggs. This is the only significant, direct negative feedback I have found in the system, and appears to be the main regulator of the acanthocephalan population in the whole ecosystem.

Kennedy (1970, 1972) suggested that temperature and diet were important factors affecting recruitment of parasites, thus the population. He was unable to find any feedback mechanisms which regulated the population of *Pomphorhynchus laevis* in dace in the River Avon. However, the acanthocephalan showed little growth in dace (Hine and Kennedy, 1974b) and very few gravid female acanthocephalans (20/1864) were recovered from dace (Hine and Kennedy, 1974a). Perhaps, the *P. laevis*-dace system was not an appropriate system to study.

VIII. GENERAL DISCUSSION

I have shown that the patterns of infection by parasites and the resulting parasite communities in fish populations are influenced by host specificity, by seasonal factors and by the age and feeding habits of the fish hosts. In addition, the behaviour of the infective larvae and that of the host are also important. The interaction of these factors determined the pattern of species of parasites present and their abundances within the parasite community in each host species.

For parasite species which matured in more than one host species, these factors interacted in such a way that the parasite was generally much more abundant in one host species than in the others. This host species is regarded as the primary host (e.g., whitefish, for *M. salmonis*, as shown in Figure 24). Other host species in which this parasite matured, but in lesser abundance, are regarded as secondary hosts (e.g., cisco, trout, coho, pike, burbot, and walleye for *M. salmonis*).

The same type of analysis can be made for larval parasites (i.e., those for which the fish is a necessary intermediate host); that host species which harbours the greatest proportion of the larval stages is regarded as the primary host, others as secondary hosts.

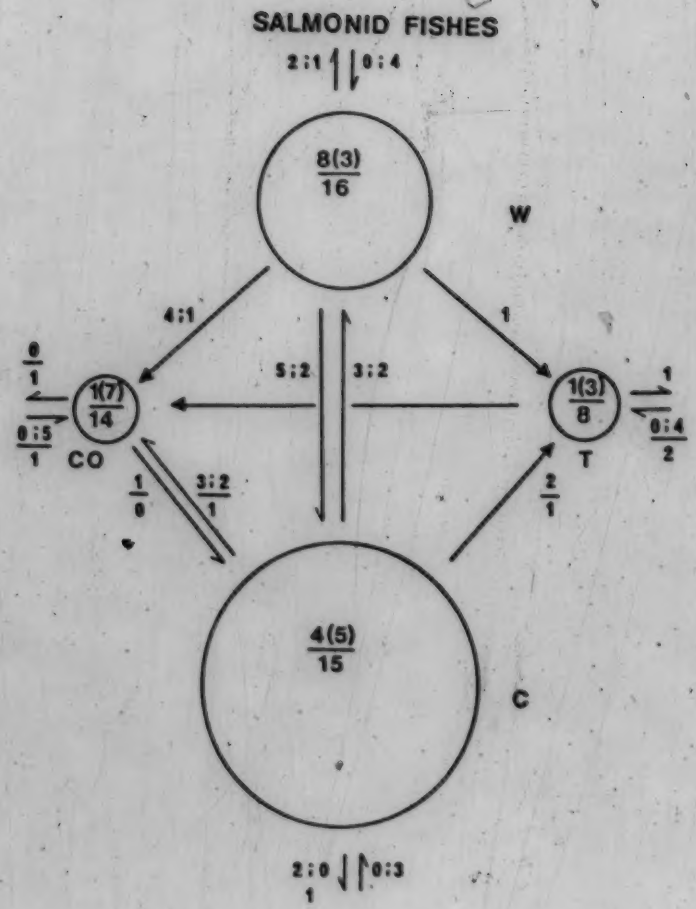
The species of parasite assigned to different categories in each species of fish examined are shown in Table 26. In the primary and secondary host categories, larval parasites are in parentheses. Parasite species found in a host species, in a stage which could mature, but did not, are listed in the "Immature" category.

Whitefish are the primary hosts for the highest number of mature parasites (8), trout and coho for the least (1 each). Sticklebacks are

Figure 24. The number of species of parasites exchanged in a community of fishes in Cold Lake, Alberta. The exchanges within each of two subcommunities are shown separately. The sizes of the circles representing each host are proportional to the host population. Numbers within the circles are number of species mature in primary host (number of species mature in secondary host)/total number of species in that species of host. Arrows indicate exchange from a primary to a secondary host. Arrows leading to and from the periphery are exchanged with the other subcommunity. Values along arrows are the number of species which mature in the recipient host (number of species which do not mature)/number of species transferred from an intermediate or transport host to a definitive host. Where the number in parentheses in the numerator or the denominator is zero, it has been omitted. See text for detailed explanation.

Salmonid fishes: W - whitefish; C - cisco; T - lake trout; CO - coho salmon.

Non-salmonid fishes: P - pike; Ws - white sucker; Ln - longnose sucker; B - burbot; ST - ninespine sticklebacks; W - walleye.


SALMONID FISHES
2;1
0;4
8(3)
16
W
4;1
1
5;2
3;2
0
1
0;5
1
1(7)
14
CO
1(3)
8
T
1
1
0;4
2
1
0
3;2
1
2
1
4(5)
15
C
2;0
1
0;3

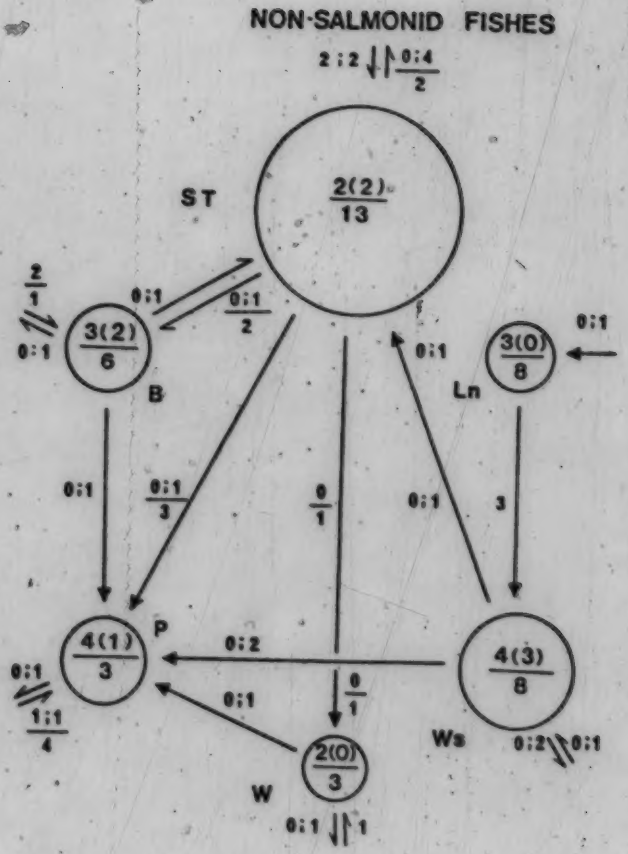

NON-SALMONID FISHES
2;2
0;4
2
ST
2(2)
13
2
1
0;1
3(2)
6
B
0;1
0;1
2
0;1
0;1
3(0)
8
Ln
0;1
0;1
0;1
3
0;1
3
0
1
4(1)
3
P
0;2
4(3)
8
Ws
0;1
1;1
4
0;1
0
1
2(0)
3
W
0;2
0;1
0;1
1

Table 26. Categorization of the parasites in different species of fish in Cold lake, Alberta

	Primary	Secondary	Immature
Whitefish	*Diesocotyle sagittata* *Phyllodistomum coregoni* *Cyathocephalus truncatus* *Proteocephalus exiguus* *Cystidicola stigmatura* *Metechinorhynchus salmonis* *Salmincola extensus* *Salmincola extensoons*	*Crepidostomum farionis* *Ergasilus auritus* *Ergasilus nerkas* *(Cotylurus erraticus)* *(Diplostomum spathaceum)* *(Diphyllobothrium sp.)*	*Pomphorhynchus bulbocolli* *Proteocephalus spp.*
Cisco	*Crepidostomum farionis* *Proteocephalus filicollis* *Ergasilus auritus* *Ergasilus nerkas* *(Diphyllobothrium sp.)* *(Triaenophorus crassus)*	*Diesocotyle sagittata* *Cyathocephalus truncatus* *Philonema agubernaculum* *Metechinorhynchus salmonis* *Salmincola extensus* *(Cotylurus erraticus)*	*Cystidicola stigmatura* *Pomphorhynchus bulbocolli* *Proteocephalus spp.*
Trout	*Eubothrium salvelini*	*Metechinorhynchus salmonis* *Ergasilus auritus* *Ergasilus nerkas* *(Diplostomum spathaceum)* *(Triaenophorus nodulosus)* *(Raphidascaris sp.)*	*Pomphorhynchus bulbocolli*
Coho	*Philonema agubernaculum*	*Diesocotyle sagittata* *Crepidostomum farionis* *Cyathocephalus truncatus* *Cystidicola stigmatura* *Metechinorhynchus salmonis* *Ergasilus auritus* *Ergasilus nerkas* *(Diphyllobothrium sp.)* *(Triaenophorus nodulosus)*	*Eubothrium spp.* *Neoechinorhynchus strigosum* *Pomphorhynchus bulbocolli* *Proteocephalus spp.*
Pike	*Proteocephalus pinguis* *Triaenophorus nodulosus* *Triaenophorus crassus* *Raphidascaris sp.*	*Metechinorhynchus salmonis* *(Schistocephalus solidus)*	*Neoechinorhynchus strigosum* *Proteocephalus spp.*
Whitesucker	*Lissorchis attenuatum* *Ihenterella sp.* *Neoechinorhynchus strigosum* *Pomphorhynchus bulbocolli*	*Caryophyllaeus sp.* *Rhabdochona cascadilla* *Ergasilus sp.*	*Metechinorhynchus salmonis*
Longnose sucker	*Caryophyllaeus sp.* *Rhabdochona cascadilla* *Ergasilus sp.*		*Metechinorhynchus salmonis*
Burbot	*Eubothrium rugosum* *Haplonema sp.* *Cystobranchus verrilli*	*Cyathocephalus truncatus* *Metechinorhynchus salmonis* *(Triaenophorus nodulosus)*	
Stickleback	*Eunodera luciopercae* *Gyrodactylus sp.* *(Cotylurus erraticus)* *(Diplostomum spathaceum)* *(Apatemon gracilis)* *(Schistocephalus solidus)* *(Triaenophorus nodulosus)* *(Raphidascaris sp.)*	*Proteocephalus filicollis* *Ergasilus auritus*	*Pomphorhynchus bulbocolli* *Eubothrium spp.* *Metechinorhynchus salmonis*
Walleye	*Proteocephalus sp.* *Bothriocephalus cuspidatus*		*Metechinorhynchus salmonis*

the primary hosts for the most species of larval parasites (6). Coho acted as a secondary host to the largest number of species of parasites (9).

It is apparent that there is a fair amount of exchange of parasites within the community of fishes. This exchange of species of parasites among host species is illustrated in Figure 24, in which the salmonid and non-salmonid portions of the community are shown separately. The size of the circles represents the proportion of the host species within the community of fishes, as given in Table 26. The values within each circle are:

$$\frac{\text{number of species mature, in primary host}}{\text{(number of species mature, in secondary host)}}$$
$$\text{total number of species in that host}$$

The arrows between species in each portion of the community indicate the direction of exchange of parasites, from primary to secondary or "immature" hosts. Values along each arrow are:

$$\frac{\text{number of species which mature in recipient;}}{\text{number which do not mature in recipient}}$$
$$\text{number of species transferred from intermediate or transport host to a definitive host}$$

The short arrows peripheral to the circles indicate transfer to or from the other portion of the community.

The Figure shows that there is a considerable amount of exchange of parasites within the salmonids, especially between the two most abundant native species, whitefish and cisco. These two species exchange 11 out of the 14 species (12 of which mature in one or both) for which one is the primary host. Trout appear to be somewhat isolated from this

exchange; they are the primary host for only a single species, which is not shared with the other native salmonids, and acquire only three (including *M. salmonis*) of the 14 species for which the native salmonids are the primary host.

The introduced coho are the primary host for only one species, *P. agubernaculum*, which is shared only with cisco. However, coho acquired almost all of the parasites for which the other salmonids are the primary host; seven of the eleven parasites matured in coho. In total, there are 16 species for which salmonids are the primary host; 13 of these are shared by two or more of the salmonids.

Another measure of the extent of the exchange between salmonids is the number of species shared per pair of host species. This number ranged from one to eleven, with a mean of 4.3. In contrast, the same measure applied to the exchange between non-salmonid fishes ranged from zero to three, with a mean of 0.7. Of the 24 species of parasites for which non-salmonids are the primary hosts, only 12 are shared by two or more species of non-salmonid fishes. These two features indicate the restricted exchange of parasites between non-salmonid fishes.

The greatest exchange, and the only one in which the parasites mature in both species, is between the two cyprinids. In this case, white suckers acquire all three parasites for which longnose suckers are the primary host, but longnose suckers do not acquire any of the four species for which white suckers are the primary host. At present, no reason for this is apparent.

The exchanges of parasites between the two groups of fishes are quite different. The transfer of parasites of salmonids to non-salmonids involves five of the 16 species, and includes four which mature in the

non-salmonids. (However, see the discussion on *M. salmonis* (p.128) for an alternative interpretation for that species.) Two of these are spread from cisco to sticklebacks, thus involving the two most abundant species of fish in the lake. On the other hand, the transfer of parasites from non-salmonids to salmonids involves six of the 24 species, but none mature in the salmonids. Most are larval forms, largely species for which sticklebacks are the primary intermediate host.

In addition to these exchanges of parasites, in which the fish hosts harbour the same stage of the parasite, there are also "life cycle transfers," in which the parasites flow from intermediate or transport hosts to the definitive host. These transfers, shown as the denominators on the arrows in Figure 24, occur at approximately equal frequencies within the two groups, with rather extensive transfers between groups. The latter appears to be due to extensive feeding on sticklebacks by trout and coho, and on cisco by pike and burbot.

Special attention should be paid to the introduced coho. All eight species which matured in the coho are shared with other salmonids; included are three of the four species from salmonids which also matured in non-salmonids. One of these is the ubiquitous *M. salmonis*. Two of the remaining species are larvae, of *Diphyllobothrium* sp. (for which cisco are the primary hosts) and *T. nodulosus* (for which sticklebacks are the primary hosts). The other four species were always immature; they include two species of acanthocephalans for which suckers are the primary hosts, and plerocercoids of *Eubothrium* and *Proteocephalus* which could not be identified to species. These could have been acquired from salmonid or non-salmonid fishes. In general, then, the important parasites of coho were derived from the dominant native salmonid fishes.

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Appendix I. Indices of dominance of the parasites in each species of fish in Cold Lake, Alberta, and in the entire community of fishes

	Community		Whitefish	Cisco	Trout	Coho	Pike	White sucker	Longnose sucker	Burbot	Stickleback	Walleye
	Unwtd	Wtd										
Metechinorhynchus salmonis	75.2	52.3	79.6	9.8	91.3	91.1	19.1			92.7		
Proteocephalus spp.*	4.5	15.4	1.1	50.3		0.2	44.9					
Cyathocephalus truncatus	1.7	6.1	9.7	0.9		0.004				0.1		
Ergasilus nerkas	1.3	4.9	0.3	16.1	0.006	6.1						
Ergasilus auritus	0.9	3.3	0.1	10.4	1.5	0.6					2.2	
Gyrodactylus sp.	0.4	2.9									37.2	
Proteocephalus filicollis	0.2	2.8		9.3							1.6	
*Cotylurus erraticus***	0.5	2.8	1.9	0.08							21.3	
Cystidicola stigmatura	0.8	2.8	4.6			0.07						
Diplostomum spathaceum	0.3	2.1	0.007		0.001						26.7	
Discocotyle sagittata	0.3	1.2	1.3	1.5		0.002						
Pomphorhynchus bulbocolli	1.0	0.8						95.9				
Proteocephalus exiguus	0.1	0.5	0.9									
Metechinorhynchus salmonis (cystacanth)	2.2	0.4						80.8	69.9		1.9	14.3
Diphyllobothrium sp.**	0.03	0.3	0.0005	0.1		0.04						
*Schistocephalus solidus***	0.03	0.3					0.04				2.7	
Triaenophorus nodulosus	2.5	0.2					35.4					
Salmincola extensus	0.05	0.2	0.3	0.003								
Salmincola extumescens	0.03	0.1	0.2									
*Triaenophorus nodulosus***	0.04	0.1			0.01	0.01				0.1	1.3	
*Apatemon gracilis***	0.02	0.2									2.4	
Bunodera luciapercae	0.01	0.1									0.9	
Rhabdochona cascadilla	0.5	0.1						0.3	26.3			
*Pomphorhynchus bulbocolli**	0.02	0.1	0.009	0.2	0.001	0.06					0.07	
Eubothrium rugosum	0.8	0.1								5.4		
Philonema agubernaculum	0.2	0.1		0.2		1.7						
Eubothrium salvelini	2.6	0.1			7.1							
Caryophyllaeus sp.	0.3	0.04						0.4	10.5			
*Cystidicola stigmatura**	0.003	0.04		0.1								
Eubothrium spp.*	0.01	0.03				0.04					0.4	
Crepidostomum farionis	0.01	0.03	0.0009	0.09		0.09						
Bothriocephalus cuspidatus	0.6	0.02										52.9
Ergasilus sp.	0.1	0.02						0.7	3.3			
Haplonema sp.	0.2	0.02								1.5		
Phyllodistomum oregoni	0.004	0.02	0.03									
Proteocephalus sp.* (A)	0.4	0.01										32.8
*Triaenophorus crassus***	0.0007	0.008			0.03							
Liescohie attenuatus	0.03	0.007						0.8				
Metechinorhynchus strigosum	0.03	0.007						0.8				
Proteocephalus pinguis	0.03	0.002					0.4					
Hunterella sp.	0.007	0.002						0.2				
Raphidascaris sp.*	0.01	0.001			0.03						8.02	
Cystobranchus verrilli	0.02	0.001								8.1		
*Metechinorhynchus strigosum**	0.007	0.0004				0.01	0.87					
Triaenophorus crassus	0.004	0.0003					0.85					
Raphidascaris sp.	0.004	0.0005					0.05					

*Immature.

**Larval.

Appendix II. Comparison of the parasite communities in different age classes of lake whitefish

AGE / PARASITES	II	III	IV	V	VI	VII	VIII	IX	X
Diacoocotyle sagittata	24.3 (2.4)[A]	80.6 (3.6)	74.4 (5.7)	75.6 (5.9)	73.1 (4.4)	60.8 (3.6)	70.4 (3.0)	62.8 (3.6)	89.5 (2.6)
Crepidostomum farionis	0	0	0	1.2 (1.0)	0	0.4 (1.0)	0.8 (1.0)	0	0
**Cotylurus erraticus*	8.1[C]	33.3	47.4	53.6	41.8	43.6	31.3	53.1	68.4
**Diplostomum spathaceum*	0	0	1.3 (1)	1.2 (1)	3.3 (1)	0	2.1 (1)	0.8 (1)	0
Phyllodistomum conrgosi	0	0	6.4 (4.2)	2.4 (1.5)	4.3 (3.0)	0.7 (1.0)	1.3 (2.3)	6.8 (1.0)	5.3 (2)
Proteocephalus exiguus	13.5 (9.6)	38.9 (16.3)	32.1 (9.3)	29.3 (18.7)	16.1 (11.6)	6.1 (10.3)	6.3 (8.5)	8.5 (7.1)	10.5 (2)
**Proteocephalus* spp.	10.8 (11.5)	16.7 (9.3)	21.8 (10.5)	25.6 (24.1)	16.1 (21.1)	14.2 (4.6)	17.5 (8.7)	16.2 (4.9)	15.8 (4)
Cyathocephalus truncatus	24.3 (3.1)	55.6 (7.3)	69.2 (12.0)	72.0 (23.3)	73.1 (18.9)	75.6 (26.8)	78.3 (18.4)	80.8 (40.6)	84.2 (20.9)
**Diphyllobothrium* sp.	0	0	0	0	0	0	0.4 (1.0)	1.5 (1.0)	0
Cystidicola stigmatura	43.2 (9.0)	83.3 (8.9)	79.5 (8.5)	74.4 (9.9)	73.1 (9.7)	72.3 (13.4)	79.6 (15.2)	79.2 (13.4)	89.5 (13.1)
Metechinorhynchus salmonis	83.8 (7.1)	100 (43.5)	98.7 (68.2)	100 (113.5)	100 (126.5)	100 (189.4)	100 (205.1)	100 (265.3)	100 (241.5)
**Pomphorhynchus bulbocolli*	5.4 (3.5)	0	0	0	1.1 (1.0)	1.4 (2.0)	0.4 (5.0)	0	0
Ergasilus nerkae	40.5 (15.7)	5.6 (13.0)	6.4 (2.6)	4.9 (38.0)	4.3 (3.5)	3.4 (9.2)	2.1 (4.8)	0.8 (17.0)	5.3 (3.0)
Ergasilus auritus	10.8 (10.8)	5.6 (11.5)	0	0	0	0.7 (3.0)	0.8 (67.0)	0.8 (17.0)	0
Salmincola extensus	5.4 (1.0)	30.6 (1.4)	52.6 (1.8)	45.1 (1.7)	39.8 (1.9)	25.0 (1.8)	24.5 (1.9)	20.8 (1.6)	5.3 (1)
Salmincola extensicorne	2.7 (1.0)	8.3 (1.3)	7.7 (1.2)	8.5 (1.0)	8.6 (1.0)	24.3 (1.6)	40.8 (1.6)	54.6 (1.8)	57.9 (1.3)
n***	37	36	78	82	93	148	240	130	19
I	37	36	78	82	93	148	240	130	19
FL (cm)	17.1	24.8	30.0	32.4	37.5	39.3	41.3	42.6	43.0
S	12	11	12	13	14	13	16	15	11
$\bar{x}$	2.73[B] (±0.22)	4.67 (±0.28)	5.13 (±0.16)	5.15 (±0.15)	4.75 (±0.15)	4.47 (±0.10)	4.73 (±0.078)	5.05 (±0.12)	5.32 (±0.30)
$\bar{N}$	22.19 (±3.47)	71.11 (±10.37)	97.17 (±6.88)	160.45 (±13.46)	159.34 (±12.86)	209.28 (±9.87)	261.36 (±11.71)	318.32 (±23.97)	318.47 (±46.76)
SI	5.06	2.50	2.01	1.97	1.58	1.42	1.38	1.41	1.34
H'	1.88	1.40	1.19	1.15	0.87	0.68	0.66	0.65	0.60
E	0.75	0.58	0.48	0.45	0.33	0.26	0.24	0.25	0.25

* Larval
** Immature
*** The abbreviations are denoted as follow: No. examined (n); No. infected (I); Fork length of fish (FL); No. spp. parasites (S); Mean No. spp. parasites ($\bar{x}$); Mean No. individual ($\bar{N}$); Simpson's Index (SI); Shannon-Weaver Index (H'); Evenness (E).

A Prevalence (mean intensity)
B Mean (± S. E.)
C Prevalence only.

Appendix III. Comparison of the parasite communities in different age classes of cisco

AGE / PARASITES	I	II	III	IV	V
Discocotyle sagittata	10.9 (1.0)[A]	25.4 (2.2)	14.6 (2.0)	18.8 (2.0)	25.6 (2.6)
[4A]*Cotylurus erraticus*	0[C]	0	0	1.8	1.0
Crepidostomum farionis	2.2 (2.0)	9.5 (2.0)	4.9 (3.3)	1.8 (2.6)	1.5 (1.0)
Cyathocephalus truncatus	0	0	3.0 (1.0)	9.9 (2.6)	12.1 (18.5)
Proteocephalus filicollis	8.7 (14.3)	23.8 (9.4)	26.1 (9.6)	19.1 (14.6)	18.6 (9.8)
[4]*Proteocephalus* spp.	54.4 (8.1)	69.5 (26.3)	69.7 (35.0)	51.8 (29.6)	41.7 (16.8)
[4A]*Diphyllobothrium* sp.	17.4 (1.3)	15.9 (1.3)	17.0 (1.3)	13.5 (1.4)	16.6 (2.5)
[4A]*Triaenophorus crassus*	0	0	0	1.1 (1.3)	1.0 (1.0)
[4]*Cystidicola stigmatura*	0	0	0.6 (1.0)	1.4 (4.8)	1.0 (1.0)
Philonema agubernaculum	0	0	0	0.6 (4.0)	2.0 (4.3)
Metechinorhynchus salmonis	10.9 (5.0)	28.6 (8.2)	26.1 (10.6)	34.8 (8.1)	38.2 (8.8)
[4]*Pomphorhynchus bulbocolli*	0	4.8 (1.7)	1.8 (2.0)	1.1 (4.7)	0
Ergasilus auritus	30.4 (7.1)	34.9 (10.9)	34.6 (13.8)	21.6 (13.3)	18.6 (10.2)
Ergasilus nerkae	17.4 (36.1)	46.0 (24.7)	29.7 (17.7)	31.9 (8.2)	40.2 (12.5)
Salmincola extensus	0	0	0	0.4 (1.0)	0
n***	46	63	165	282	199
I	36	55	158	249	174
S	8	9	12	15	13
$\bar{S}$	2[B] (±0.21)	2.89 (±0.16)	2.41 (±0.10)	2.38 (±0.08)	2.54 (±0.11)
$\bar{N}$	19.43[B] (±4.61)	42.95 (±6.61)	43.30 (±6.61)	31.45 (±4.48)	25.84 (±3.25)
SI	3.45	3.24	2.49	2.84	5.19
H'	1.45	1.43	1.29	1.45	1.84
E	0.69	0.65	0.51	0.53	0.71

See Appendix II for abbreviations and format.

Appendix IV. Seasonal variation in the parasite communities in group A lake whitefish (age classes IV and V)

MONTHS / PARASITES	J	F	M	A	M	J	J	A	S	O	N	D
Diecocotyle sagittata	76 (6)[A]	50 (3)	83.3 (5.2)	75 (1)	56.3 (4.7)	85 (5.1)	73.1 (5.8)	100 (6.9)	66.7 (6.3)	66.7 (5)	83.3 (5)	61.9 (7.5)
**Cotylurus erraticus*	75[C]	100	66.7	25	56.3	35	34.6	37.5	66.7	0	100	61.9
Cyathocephalus truncatus	75 (67.7)	100 (29.5)	100 (6.5)	50 (1.5)	81.3 (7.8)	75 (11.9)	65.4 (12.6)	37.5 (2.3)	66.7 (25)	66.7 (9)	83.3 (16.8)	95.2 (33.9)
Phyllodistomum coregoni	0	0	0	0	23.1 (3)	0	3.9 (1)	0	0	0	0	0
Proteocephalus exiguus	0	0	16.7 (1)	0	23.1 (59)	25 (32)	57.7 (11.9)	37.5 (6.7)	50 (6.7)	33.3 (8)	16.7 (1)	0
**Proteocephalus* spp.	62.5 (38.4)	50 (2)	50 (8)	25 (1)	31.3 (37.6)	30 (10)	11.5 (12)	0	16.7 (1)	0	33.3 (34)	42.9 (11.6)
Cysticola stigmatura	100 (11.6)	100 (19)	100 (23.2)	75 (10.3)	93.8 (10.2)	90 (10.7)	69.2 (4.9)	37.5 (4.3)	66.7 (3.3)	66.7 (4)	83.3 (8.6)	90.5 (10.1)
Metechinorhynchus salmonis	75 (171.7)	100 (98.5)	100 (87.3)	100 (71.3)	93.8 (88.1)	100 (71.2)	100 (101.8)	100 (103.6)	83.3 (96.6)	100 (57.3)	100 (93)	100 (138.4)
Ergasilus nerkae	0	0	0	0	0	10 (1.5)	0	0	0	0	0	0
Salmincola extensus	25 (3)	0	50 (1.7)	50 (1)	56.3 (1.7)	50 (2.4)	61.5 (1.3)	50 (1.3)	33.3 (1.5)	66.7 (1.5)	66.7 (2)	47.6 (1.8)
Salmincola extumescens	0	0	16.7 (1)	25 (1)	0	0	3.9 (1)	25 (1)	0	0	0	0
n[***]	8	2	6	4	16	20	26	8	6	3	6	21
I	8	2	6	4	16	20	26	8	6	3	6	21
S	7	6	9	8	9	9	10	8	8	6	8	7
$\bar{x}$	5.38[B] (±0.38)	5.0 (±1.0)	5.83 (±0.40)	4.50 (±0.29)	5.19 (±0.31)	5.0 (±0.23)	4.77 (±0.28)	4.50 (±0.63)	4.67 (±1.02)	4.33 (±1.2)	5.67 (±0.42)	5.0 (±0.25)
$\bar{N}$	224.58 (±40.3)	155.5 (±80.5)	130.83 (±40.47)	87.25 (±29.05)	129.94 (±22.94)	108.3 (±15.39)	128.92 (±21.01)	119.88 (±18.61)	117.83 (±44.37)	75 (±50.85)	128.83 (±33.60)	193.95 (±35.48)
SI	2.52	2.18	2.04	1.33	2.26	2.19	1.58	1.30	1.81	1.59	1.87	1.84
H'	1.21	1.05	1.09	0.56	1.27	1.24	0.88	0.57	0.96	0.84	1.05	0.96
E	0.62	0.58	0.49	0.27	0.58	0.56	0.38	0.27	0.46	0.47	0.51	0.49

See Appendix II for abbreviations and format

Appendix V. Seasonal variations in the parasite communities in group B lake whitefish (age classes VII and VIII)

MONTHS / PARASITES	J	F	M	A	M	J	J	A	S	O	N	D
Discocotyle sagittata	61.5 (3.6)[A]	73.3 (2.3)	57.1 (3.3)	61.9 (3.2)	73.9 (2.1)	60 (3.7)	67.9 (3.1)	73.3 (3.2)	73.1 (3.8)	76.2 (2.5)	74.2 (3.9)	50 (3.5)
**Cotylurus erraticus*	69.2[C]	60	40.5	71.4	85.2	51.1	56.6	42.2	26.9	28.6	51.6	41.7
Cyathocephalus truncatus	92.3 (42.8)	73.3 (52.2)	85.7 (18.3)	61.9 (4.2)	95.7 (22)	84.4 (41.5)	69.8 (53.1)	60 (24.5)	46.2 (15.2)	76.2 (16.5)	87.1 (26.3)	91.7 (46.8)
**Diphyllobothrium* sp.	0	0	0	0	0	0	0	0	0	4.8 (1)	0	0
**Diplostomum spathaceum*	0	0	0	0	0	0	9.4 (1)	0	0	0	0	0
Phyllodistomum oregoni	7.7 (1)	0	0	9.5 (1)	4.3 (1)	0	1.9 (5)	0	0	0	0	0
Proteocephalus exiguus	0	0	7.1 (14.3)	0	13 (7.7)	8.9 (11.8)	22.6 (5.8)	2.2 (2)	0	0	0	0
**Proteocephalus* spp.	76.9 (37.7)	33.3 (5)	21.4 (23.8)	33.3 (2.6)	21.7 (3.8)	26.7 (3.9)	5.7 (4)	0	0	4.8 (1)	3.2 (15)	19.4 (5.7)
Cystidicola stigmatura	92.3 (28.5)	100 (16.4)	85.7 (25.9)	100 (19.1)	78.3 (11.3)	80 (12.2)	54.7 (5.2)	55.6 (3.6)	61.5 (2.8)	76.2 (7.4)	87.1 (14.9)	88.9 (18)
Metechinorhynchus salmonis	100 (218.5)	100 (176.2)	100 (146.6)	100 (88.8)	100 (189.8)	100 (226)	100 (269.9)	100 (163.4)	100 (102.8)	100 (144.4)	100 (254.7)	100 (258.3)
**Pomphorhynchus bulbocolli*	0	0	2.4 (3)	0	0	0	0	0	3.8 (1)	0	0	0
Ergasilus auritus	0	13.3 (12)	0	0	0	0	0	0	0	0	0	2.8 (113)
Ergasilus nerkae	0	0	0	0	0	0	0	22.2 (7)	0	0	0	0
Salmincola extensus	53.8 (1.3)	13.3 (2)	42.9 (1.8)	33.3(1.1)	34.8 (1.5)	28.9 (1.5)	24.5 (1.9)	28.9 (2.1)	19.2 (1.2)	23.8 (1.8)	38.7 (3.4)	13.9 (1.2)
Salmincola extenuatus	23.1 (2.3)	40 (1.3)	21.4 (1.6)	47.6 (1.9)	47.8 (2.2)	48.9 (1.9)	22.6 (1.3)	37.8 (1.7)	34.6 (1.8)	9.6 (1.3)	25.9 (1.1)	27.8 (1.3)
n	13	15	42	21	23	45	53	45	26	21	31	36
I	13	15	42	21	23	45	53	45	26	21	31	36
S	9	9	10	9	10	9	11	9	8	9	8	9
$\bar{x}$	5.85 (±0.30)	5.21 (±0.26)	4.60 (±0.21)	5.24 (±0.3)	5.35 (±0.24)	4.93 (±0.18)	4.40 (±0.16)	4.00 (±0.16)	3.65 (±0.22)	4.05 (±0.26)	4.68 (±0.21)	4.48 (±0.22)
$\bar{y}$	322.31 (±40.14)	256.6 (±39.72)	196.93 (±16.0)	120.43 (±12.99)	229.91 (±31.60)	274.46 (±21.86)	318.92 (±30.05)	188.69 (±20.93)	117.46 (±20.24)	168.0 (±26.88)	299.74 (±30.29)	336.4 (±33.08)
H'	2.04	1.78	1.73	1.75	1.43	1.50	1.37	1.32	1.30	1.33	1.37	1.55
H	1.07	0.91	0.93	0.91	0.71	0.72	0.58	0.58	0.55	0.57	0.61	0.75
E	0.49	0.41	0.40	0.41	0.31	0.33	0.24	0.26	0.26	0.29	0.34	

See Appendix II for abbreviations and format

Appendix VI. Seasonal variations in the parasites communities in cisco (age classes IV and V)

MONTHS / PARASITES	J	F	M	A	M	J	J	A	S	O	N	D
Discocotyle sagittata	34.5 (1.9)[A]	41.3 (2)	17.5 (1.6)	29.4 (1.6)	20.6 (4.3)	8.7 (2.7)	11.3 (1.4)	10.4 (2.1)	37.5 (2)	53.6 (2.4)	29 (2.4)	22.9 (2.8)
**Cotylurus erraticus	3.4[B]	0	0	2.9	8.8	0	0	1.5	0	0	3.2	0
Crepidostomum farionis	0	0	0	0	0	0	0	0	0	3.6 (1)	0	0
Cyathocephalus truncatus	0	23.5 (11.5)	10 (6.3)	2.9 (9)	14.7 (12.2)	4.3 (1.7)	6.5 (3.5)	11.9 (2.3)	5 (1)	25 (4)	9.7 (1.7)	17.1 (3)
**Diphyllobothrium sp.	13.8 (2.3)	0	30 (2.3)	38.2 (1.8)	23.5 (3.3)	15.9 (1.5)	6.5 (1.3)	11.9 (1.5)	75 (1.7)	14.3 (1.5)	9.7 (1)	8.6 (1.3)
Proteocephalus filicollis	17.2 (7.4)	0	5 (7)	0	23.5 (11.1)	7.2 (17.8)	19.4 (8.4)	52.2 (17.5)	47.5 (10.6)	10.7 (1)	54.8 (7.2)	5.7 (2.5)
*Proteocephalus spp.	13.8 (3.8)	0	65 (22.5)	44.1 (151.3)	32.4 (29.6)	46.4 (19.4)	50 (17.6)	52.2 (10.3)	67.5 (8.8)	14.3 (12.8)	9.7 (1)	77.1 (20.9)
**Triaenophorus crassus	0	0	0	0	0	1.4 (1)	0	1.5 (1)	2.5 (2)	0	6.5 (1)	0
*Cystidicola stigmatura	0	0	5 (3.5)	5.9 (1)	11.8 (1.5)	0	1.6 (1)	0	0	0	0	0
Philonema agubernaculum	6.9 (3.5)	0	0	2.9 (5)	0	0	3.2 (5)	0	0	0	0	0
Metechinorhynchus salmonis	37.9 (4.8)	41.3 (7.1)	32.5 (8)	26.5 (11.1)	38.2 (6.5)	42 (4.3)	33.9 (7.9)	34.3 (7.8)	37.5 (7.9)	50 (20.1)	35.5 (8.2)	40 (12.4)
Pomphorhynchus bulbocolli	0	0	0	0	0	0	1.6 (1)	3 (4.5)	0	3.6 (5)	0	0
Ergasilus auritus	17.2 (3.2)	35.3 (2.3)	40 (5.1)	35.3 (25.7)	35.3 (19.1)	13 (18.9)	14.5 (4.7)	9.0 (7.8)	22.5 (12.6)	32.1 (16)	9.7 (1.7)	5.7 (4.5)
Ergasilus nerkae	27.6 (4)	35.3 (1.5)	35 (3.6)	26.5 (1.9)	17.6 (4.2)	8.7 (10.7)	19.4 (44.4)	50.7 (7.6)	80 (23.5)	78.6 (11.7)	22.6 (5.6)	45.7 (4.6)
Salvelinicola eatoni	0	0	0	0	0	0	0	0	0	3.6 (1)	0	0
n[***]	29	17	40	34	34	69	62	67	40	28	31	35
I	23	15	36	27	28	56	50	57	40	25	30	34
S	9	9	9	10	10	10	12	11	10	10	10	8
$\bar{S}$	2.26[C] (±0.23)	2.00 (±0.24)	2.64 (±0.26)	2.70 (±0.37)	2.73 (±0.25)	1.91 (±0.14)	2.12 (±0.18)	2.70 (±0.18)	3.05 (±0.22)	3.24 (±0.29)	2.00 (±0.21)	2.29 (±0.20)
$\bar{N}$	8.20 (±2.16)	8.87 (±4.08)	24.75 (±5.86)	101.74 (±35.64)	31.43 (±7.61)	20.02 (±4.04)	19.65 (±2.70)	24.47 (±3.12)	37.45 (±11.55)	32.58 (±5.64)	9.87 (±2.23)	25.91 (±3.96)
SI	6.03	3.48	2.24	1.44	4.41	2.78	3.3	3.79	3.09	3.87	3.49	2.13
H'	1.96	1.39	1.27	0.67	1.77	1.40	1.44	1.56	1.43	1.56	1.52	1.09
E	0.89	0.86	0.57	0.29	0.77	0.60	0.57	0.64	0.62	0.67	0.65	0.52

See Appendix II for abbreviations and format

Appendix VII. Comparison of the food of different age classes of lake whitefish

Food Items \ Age	II	III	IV	V	VI	VII	VIII	IX
Stickleback	0*	0	0	2.0	6.1	0	1.3	3.5
Nematomorpha	0	0	0	0	6.1	0	0	0
Glossiphoniidae	12.1	18.8	13.6	7.8	9.1	8.5	13.2	5.2
Mysis relicta	0	0	0	0	0	0	1.3	0
Pontoporeia affinis	51.5	37.5	68.2	60.8	60.6	74.5	77.6	89.7
Hyallela azteca	12.1	18.8	9.1	9.8	12.1	4.3	14.5	10.3
Gammarus lacustris	3.0	43.8	11.4	23.5	15.2	21.3	25.0	12.1
Ephemeroptera	9.1	0	4.6	0	0	6.4	0	1.7
Corixidae	0	0	0	0	0	6.4	0	0
Trichoptera	0	12.5	6.8	7.8	3.0	19.1	21.1	15.5
Tendipedidae	48.5	68.8	63.6	37.3	42.4	46.8	56.6	53.5
Physidae	0	0	9.1	7.8	3.0	8.5	1.3	3.5
Planorbidae	0	0	0	0	0	0	0	1.7
Sphaeriidae	42.4	56.3	65.9	52.9	63.6	66.0	68.4	72.4
Fish egg	0	0	11.4	21.6	15.2	17.0	6.6	6.9
Vegetation	0	0	4.6	2.0	15.2	6.4	4.0	1.7
n**	41	25	59	62	43	53	119	86
IF	33	16	44	51	33	47	76	58
SF	7	6	11	11	12	12	12	13
$\overline{SF}$ (±S.E.)	1.85*** (±0.12)	2.63 (±0.18)	2.75 (±0.16)	2.33 (±0.15)	2.64 (±0.20)	2.81 (±0.71)	2.93 (±0.14)	2.84 (±0.16)
SI	4.44	4.99	5.41	5.88	6.15	6.03	5.48	4.65
H'	1.64	1.69	1.94	1.98	2.09	2.06	1.92	1.85
E	0.82	0.94	0.77	0.80	0.79	0.81	0.75	0.66

*Prevalence - percentage, out of stomach with some food.

**The abbreviations are denoted as follow: No. examined (n); No. with food (IF); No. food items (SF); Mean no. food items ($\overline{SF}$); Simpson's index (SI); Shannon-Weaver index (H'); Evenness (E).

***Mean (±S.E.).

Appendix VIII. Seasonal variations in the food of group A lake whitefish (age classes IV and V)

Food Items \ Months	J	F	M	A	M	J	J	A	S	O	N	D
Stickleback	0*	0	0	0	0	0	0	0	0	0	16.7	0
Glossiphoniidae	0	0	0	0	16.7	0	21.1	28.6	50	0	0	0
Mysis relicta	0	50	0	25	0	0	0	0	0	0	0	0
Pontoporeia affinis	75	100	0	25	66.7	100	68.4	71.4	75	0	50	35
Hyallela azteca	0	0	0	0	25	0	0	28.6	0	33.3	16.7	5
Gammarus lacustris	12.5	0	0	0	8.3	0	10.5	42.9	0	100	33.3	45
Ephemeroptera	0	0	0	0	25	0	0	0	0	0	0	0
Trichoptera	12.5	0	0	0	16.7	0	5.3	0	0	0	0	15
Tendipedidae	12.5	50	0	25	66.7	92.9	68.4	57.1	75	0	16.7	10
Physidae	0	0	0	0	8.3	0	15.8	28.6	25	33.3	0	0
Sphaeriidae	12.5	50	0	25	83.3	78.6	89.5	42.9	75	33.3	66.7	20
Fish Eggs	12.5	0	0	0	0	0	0	0	0	0	0	80
Vegetation	0	0	0	0	0	0	10.5	0	0	0	0	0
n**	9	2	6	4	16	16	25	8	6	3	6	21
IF	8	2	0	1	12	14	19	7	4	3	6	20
SF	6	4	0	4	9	3	8	7	5	4	6	7
$\overline{SF}$	1.38***	2.5	0	4.0	3.17	2.71	2.89	3.0	3.0	2.0	2.0	2.1
(±S.E.)	(±0.26)	(±1.5)			(±0.37)	(±0.16)	(±0.21)	(±0.44)	(±0.71)		(±0.37)	(±0.19)
SI	2.95	3.57	0	4	5.64	3.0	4.58	6.21	4.5	3.0	4.5	4.24
H'	1.42	1.33	0	1.39	1.91	1.10	1.71	1.89	1.55	1.24	1.63	1.64
E	0.76	0.96	0	1.0	0.86	1.0	0.81	0.97	0.96	0.89	0.90	0.83

*Prevalence - percentage, out of stomach with some food.

**The abbreviations are denoted as follow: No. examined (n); No. with food (IF); No. food items (SF); Mean no. food items ($\overline{SF}$); Simpson's index (SI); Shannon-Weaver index (H'); Evenness (E).

***Mean (±S.E.).

Appendix IX. Seasonal variation in food of group B lake whitefish (age classes VII and VIII)

Food Items \ Months	J	F	M	A	M	J	J	A	S	O	N	D
Stickleback	0*	0	11.1	0	0	0	0	0	0	0	0	0
Glossiphoniidae	0	0	0	0	23.5	27.8	8.3	0	0	36.4	0	0
Mysis relicta	16.7	0	0	0	0	0	0	0	0	0	0	0
Pontoporeia affinis	50	66.7	11.1	87.5	76.5	100	100	83.3	100	63.6	92.3	66.7
Hyallela azteca	0	0	66.7	12.5	23.5	5.6	8.3	0	0	0	0	0
Gammarus lacustris	33.3	0	66.7	25	41.2	5.6	8.3	0	0	27.3	7.7	27.8
Ephemeroptera	0	0	0	0	5.9	5.6	0	0	0	0	0	0
Corixidae	0	0	0	0	0	5.6	0	0	0	9.1	0	0
Trichoptera	33.3	33.3	11.1	75	35.3	11.1	0	0	0	9.1	15.4	27.8
Tendipedidae	33.3	33.3	33.3	25	76.5	77.8	83.3	66.7	50	9.1	53.8	44.4
Physidae	0	0	11.1	0	5.9	5.6	0	0	0	9.1	0	5.6
Sphaeriidae	50	33.3	44.4	50	76.5	83.3	66.7	83.3	50	90.9	84.6	50
Fish Eggs	16.7	33.3	0	0	0	0	0	0	0	0	0	72.2
Vegetation	0	0	22.2	0	0	5.6	8.3	0	0	9.1	0	5.6
n**	7	3	16	16	18	31	22	14	4	12	14	18
IF	6	3	9	8	17	18	12	6	2	11	13	18
SF	7	5	9	6	9	11	7	3	3	9	5	8
$\overline{SF}$	2.17***	2.0	2.78	2.75	3.65	3.33	2.83	2.33	2.0	2.64	2.54	3.0
(±S.E.)	(±0.48)	(±0.58)	(±0.43)	(±0.45)	(±0.31)	(±0.28)	(±0.27)	(±0.42)	(±1.0)	(±0.2)	(±0.22)	(±0.27)
SI	6.13	4.50	5.95	4.4	6.14	4.62	3.70	2.97	2.67	4.70	3.41	5.72
H′	1.87	1.56	1.95	1.61	1.94	1.78	1.48	1.09	1.04	1.80	1.34	1.85
E	0.96	0.97	0.88	0.89	0.88	0.72	0.74	1.0	0.94	0.80	0.82	0.88

*Prevalence - percentage, out of stomach with some food.
**The abbreviations are denoted as follow: No. examined (n); No. with food (IF); No. food items (SF); Mean no. food items ($\overline{SF}$); Simpson's index (SI); Shannon-Weaver index (H′); Evenness (E).
***Mean (±S.E.).

Appendix X. Seasonal variations in food of cisco (age classes IV and V).

Food Items \ Months	J	F	M	A	M	J	J	A	S	O	N	D
Stickleback	0*	0	0	0	5.3	8.3	0	0	0	10.5	4.8	0
Copepoda	0	0	75	25	10.5	75	57.9	21.4	0	42.1	85.7	50
Mysis relicta	66.7	75	25	75	10.5	16.7	15.8	7.1	100	47.4	9.5	6.3
Pontoporeia affinis	33.3	25	0	25	0	0	5.3	7.1	0	15.8	0	6.3
Hyallela azteca	0	0	0	0	42.1	0	5.3	7.1	0	0	0	0
Gammarus lacustris	0	0	0	0	36.8	8.3	5.3	57.1	0	15.8	9.5	6.3
Ephemeroptera (L)	0	0	0	0	47.4	8.3	10.5	7.1	0	0	4.8	0
Ephemeroptera (a)	0	0	0	0	0	0	5.3	7.1	0	0	0	5.3
Odonata	0	0	0	0	5.3	0	0	0	0	0	0	0
Diptera	0	0	0	0	0	0	0	7.1	0	0	0	0
Sphaeriidae	0	0	0	0	0	0	0	0	0	15.8	0	0
Fish Eggs	33.3	0	0	0	0	0	0	0	0	0	0	43.8
n**	29	17	25	18	21	30	32	25	26	26	31	43
IF	3	4	4	4	19	12	19	14	1	19	21	16
SF	3	2	2	3	7	5	7	8	1	6	5	5
$\frac{SF}{SF}$	1.33***	1.0	1.0	1.25	1.58	1.17	1.05	1.29	1.0	1.47	1.14	1.13
(± S. E.)	(±0.33)			(±0.25)	(±0.14)	(±0.11)	(±0.05)	(±0.13)		(±0.14)	(±0.1)	(±0.09)
SI	2.67	1.60	1.60	2.27	4.41	2.22	2.91	3.65	1.0	4.45	1.75	2.80
H'	1.04	0.56	0.56	0.95	1.64	1.13	1.44	1.06	0	1.63	0.90	1.21
E	0.94	0.79	0.79	0.85	0.82	0.66	0.69	0.76	1	0.90	0.49	0.72

Footnotes, see Appendix VII, for abbreviations and format.

Appendix XI. Intraintestinal distribution of *Metechinorhynchus salmonis* (and gravid females) in different age classes of lake whitefish

Age	Ave. Length of Intestine (mm)	No. Exam	Section of Intestine 1	2	3	4	5	6	7	8	9	10	Totals
2	123	31	0.27* (0)	0.6 (0)	0.4 (0)	0.4 (0)	0.23 (0)	0.13 (0)	0.57 (0.07)	0.93 (0.07)	1.6 (0.17)	0.73 (0.1)	5.86 (0.41)
3	167	24	4 (0.12)	6.16 (0.28)	4.32 (0.2)	3.88 (0.36)	1.08 (0)	0.6 (0.08)	0.84 (0.04)	4.68 (0.84)	6.56 (2.28)	1.84 (0.56)	33.96 (4.76)
4	196	46	6.67 (0.13)	13.0 (0.19)	6.83 (0.44)	5.71 (0.48)	2.08 (0.21)	1.52 (0.08)	1.79 (0.13)	9.35 (2.44)	10.35 (4.23)	1.63 (0.73)	58.93 (9.06)
5	220	59	21.46 (0.54)	34.41 (1.41)	19.47 (1.05)	10.92 (0.98)	3.92 (0.09)	2.53 (0.05)	3.10 (0.47)	9.93 (2.78)	10.69 (3.97)	2.73 (1.32)	119.16 (12.66)
6	248	36	20.2 (0.4)	30.68 (0.86)	15.78 (1.05)	9.84 (1.0)	3.41 (0.38)	2.35 (0.05)	2.92 (0.3)	10.73 (2.38)	11.0 (2.97)	1.38 (0.35)	108.29 (9.74)
7	269	40	25.8 (0.68)	53.4 (1.75)	21.9 (1.0)	13.75 (1.3)	4.3 (0.25)	2.28 (0.05)	2.6 (0.08)	11.5 (2.08)	9.68 (3.65)	2.45 (0.73)	147.66 (11.75)
8	277	76	35.3 (1.13)	58.11 (1.62)	26.05 (1.49)	15.92 (1.51)	5.61 (0.32)	3.42 (0.08)	3.13 (0.14)	10.23 (1.75)	8.2 (2.24)	2.42 (0.53)	168.44 (10.81)
9	283	66	41.3 (2.47)	99.3 (4.89)	41.86 (3.2)	22.39 (2.83)	7.73 (0.67)	4.91 (0.21)	2.83 (0.2)	8.21 (1.76)	7.64 (0.71)	2.14 (0.44)	238.31 (17.38)

*mean no. of *M. salmonis*
(mean no. of gravid females)

Appendix XII. Intraintestinal distribution of *Metechinorhynchus salmonis* (and gravid females) in group A lake whitefish taken at different seasons

Month	No. Exam	Section of Intestine 1	2	3	4	5	6	7	8	9	10	Totals
J	8	26.3* (0.1)	43.1 (1.0)	21.1 (0.4)	12.4 (0.5)	5.8 (0)	1.8 (0.1)	1.8 (0.1)	7.0 (2.8)	8.6 (4.9)	1.9 (0.9)	129.8 (10.8)
F	2	8.0 (0)	24.5 (0)	17.5 (0)	17.5 (0)	6.0 (0)	2.0 (0)	0.5 (0)	8.5 (0.5)	7.0 (2.5)	1.0 (0.5)	92.5 (3.5)
M	6	13.5 (0)	20.2 (0)	12.5 (0.5)	7.2 (0.2)	3.8 (0)	2.5 (0.2)	2.2 (0.2)	10.0 (2.2)	11.2 (3.2)	4.8 (2.0)	87.9 (8.5)
A	4	12.3 (0)	17.0 (1.0)	10.0 (1.5)	7.5 (0.5)	1.8 (0)	0.8 (0)	0 (0)	8.5 (1.8)	10.8 (6.0)	2.5 (1.0)	71.2 (11.8)
M	15	13.8 (0.1)	32.6 (1.2)	12.9 (1.7)	6.3 (1.5)	1.8 (0.3)	0.6 (0)	0.8 (0.1)	7.9 (3.5)	9.4 (3.9)	1.1 (0.4)	87.2 (12.7)
J	16	11.5 (0.3)	16.9 (0.6)	9.4 (0.6)	7.9 (0.3)	2.8 (0.8)	1.3 (0.1)	1.0 (0)	5.6 (1.1)	9.3 (3.6)	2.3 (0.9)	68 (8.3)
J	10	8.0 (0.3)	18.6 (1.6)	12.0 (0.7)	7.5 (0.1)	2.9 (0.1)	3.4 (0.1)	1.4 (0.4)	11.4 (3.4)	9.1 (2.2)	1.5 (0.4)	75.8 (9.3)
A	8	1.6 (0)	10.4 (0.6)	10.5 (1.3)	8.5 (1.6)	2.0 (0.1)	2.6 (0.1)	4.0 (0.4)	23.8 (6.3)	21.8 (5.4)	3.5 (0.6)	88.7 (16.4)
S	6	21.0 (1.0)	14.3 (0.7)	7.8 (0.8)	5.3 (0.3)	1.3 (0)	1.7 (0)	1.7 (0)	8.5 (1.7)	15.2 (7.2)	3.7 (1.8)	80.5 (13.5)
O	3	16.3 (0)	13.0 (0)	7.0 (0)	3.0 (0)	1.3 (0)	0 (0)	1.0 (0.3)	2.0 (0)	9.7 (6.7)	2.0 (1.7)	55.3 (8.7)
N	6	10.7 (0.2)	19.0 (0.2)	10.5 (0.5)	6.3 (0.3)	2.7 (0)	2.0 (0)	0.7 (0)	7.8 (1.8)	13.0 (4.5)	1.3 (0.3)	74 (7.8)
D	21	21.4 (0.1)	31.7 (1.1)	22.0 (0.9)	11.9 (1.0)	5.0 (0.05)	3.8 (0.05)	6.1 (0.7)	11.0 (3.1)	8.1 (3.8)	1.9 (1.1)	122.9 (11.9)

*Mean no. of *M. salmonis*
(Mean no. gravid female)

Appendix XIII. Intraintestinal distribution of *Metechinorhynchus salmonis* (and gravid females) in group B lake whitefish taken at different seasons

Month	No. Exam	Section of Intestine 1	2	3	4	5	6	7	8	9	10	Totals
J	7	30.4*	77.0	26.4	15.0	6.0	4.3	2.9	12.3	10.0	3.3	187.6
		(0.3)	(1.0)	(1.1)	(1.3)	(0.1)	(0)	(0.3)	(3.4)	(5.3)	(0.9)	(13.7)
F	3	24.0	59.0	36.3	22.7	8.0	4.0	4.7	13.3	8.3	1.3	181.6
		(0)	(0.7)	(0.7)	(0.7)	(0.3)	(0)	(0)	(0.7)	(0.3)	(0.3)	(3.7)
M	16	33.4	45.4	22.9	19.1	4.0	2.4	1.5	12.2	7.8	2.8	151.5
		(0.6)	(1.0)	(1.2)	(1.5)	(0)	(0)	(0)	(1.7)	(1.6)	(0.3)	(8.0)
A	7	18.7	34.0	11.0	4.3	2.1	1.3	1.1	5.7	3.4	1.3	82.9
		(0.1)	(0.7)	(0.7)	(1.0)	(0)	(0)	(0)	(0.4)	(0.6)	(0.4)	(3.9)
M	8	33.6	51.3	18.1	12.0	6.9	1.8	1.5	4.0	2.0	0.4	131.6
		(4.0)	(3.4)	(2.5)	(2.4)	(1.1)	(0.1)	(0.6)	(0.8)	(1.0)	(0.3)	(16.2)
J	7	24.0	60.1	19.7	12.9	6.9	7.1	7.6	15.4	6.9	4.1	164.7
		(0.1)	(1.7)	(1.1)	(1.6)	(0)	(0)	(0)	(0.9)	(2.1)	(0.7)	(8.2)
J	8	41.3	114.5	55.3	29.5	42.6	7.4	7.8	23.5	22.3	4.1	348.3
		(2.4)	(3.8)	(1.9)	(2.3)	(0.1)	(0)	(0)	(2.5)	(2.4)	(0.5)	(15.9)
A	11	20.0	19.3	13.4	9.0	4.4	1.5	1.4	10.5	13.5	3.9	96.9
		(1.4)	(0.3)	(1.0)	(1.0)	(0.6)	(0.2)	(0.1)	(4.0)	(6.5)	(1.5)	(16.6)
S	4	39.0	32.3	13.0	8.3	2.5	1.0	3.3	3.0	2.5	0.5	105.4
		(1.8)	(4.0)	(2.8)	(1.8)	(0)	(0.3)	(0.3)	(0.8)	(0.5)	(0.5)	(12.8)
O	12	20.8	44.7	17.0	8.2	2.8	1.9	0.8	8.3	10.0	1.8	116.3
		(0.3)	(2.0)	(1.5)	(0.3)	(0)	(0)	(0)	(1.6)	(4.4)	(0.3)	(10.4)
N	14	20.1	59.7	21.1	14.7	3.5	1.2	2.9	10.4	10.1	2.0	145.7
		(1.4)	(1.1)	(1.1)	(2.6)	(0.4)	(0.1)	(0.3)	(1.5)	(2.4)	(0.4)	(11.3)
D	18	56.8	91.7	32.2	21.3	6.8	4.2	3.9	10.6	5.6	2.3	235.4
		(0.8)	(1.2)	(0.9)	(1.7)	(0.5)	(0.1)	(0.1)	(2.1)	(1.3)	(0.6)	(9.3)

*Mean no. of *M. salmonis*
(Mean no. gravid females)

Appendix XIV. Intraintestinal distribution of *Metechinorhynchus salmonis* (and gravid females) in cisco taken at different seasons

Month	No. Exam	Section of Intestine 1	2	3	4	5	6	7	8	9	10	Totals
J	27	0.9*	2.0	2.1	1.3	0.7	0.8	1.3	2.5	3.0	0.6	15.2
		(0.1)	(0.1)	(0.4)	(0.1)	(0)	(0)	(0.4)	(1.0)	(1.5)	(0.4)	(4.0)
F	20	1.3	1.6	2.1	1.3	0.6	0.7	1.3	2.6	1.9	0.9	14.3
		(0.6)	(0.3)	(0.8)	(0.7)	(0.1)	(0.1)	(0.5)	(1.5)	(1.0)	(0.2)	(5.8)
M	14	0.4	0.8	0.7	1.2	0.1	0.4	0.4	0.6	1.7	0.1	6.4
		(0)	(0)	(0.4)	(0.3)	(0)	(0)	(0.1)	(0.3)	(0.8)	(0.1)	(2.0)
A	6	1.7	3.8	4.2	2.8	1.5	0.2	1.3	2.2	2.7	0.7	21.1
		(0)	(0.8)	(1.5)	(0.8)	(0.5)	(0)	(0.2)	(0.8)	(0.7)	(0.2)	(5.5)
M	7	0.1	0.3	0.4	0.7	0.1	0.6	0.1	0.1	2.3	2.4	7.1
		(0)	(0)	(0)	(0)	(0)	(0)	(0)	(0)	(1.3)	(0.4)	(1.7)
J	36	0.3	0.6	1.1	0.8	0.03	0.1	0.5	1.1	1.7	0.3	6.5
		(0.03)	(0.5)	(0.4)	(0.1)	(0)	(0)	(0.1)	(0.7)	(0.8)	(0.5)	(3.1)
J	57	0.9	1.5	1.4	0.5	0.2	0.3	0.5	1.3	1.8	0.4	8.8
		(0.2)	(0.4)	(0.2)	(0.2)	(0.04)	(0.1)	(0.1)	(0.6)	(0.7)	(0.1)	(2.6)
A	57	0.5	1.0	0.9	1.1	0.5	0.2	0.4	2.0	3.1	0.7	10.4
		(0.04)	(0.2)	(0.2)	(0.5)	(0.04)	(0.04)	(0.2)	(1.0)	(1.5)	(0.2)	(3.9)
S	38	0.4	0.8	0.8	0.6	0.2	0.3	0.2	1.0	1.8	1.0	7.1
		(0)	(0.1)	(0.4)	(0.2)	(0.1)	(0.03)	(0.2)	(0.4)	(0.9)	(0.4)	(2.7)
O	34	2.9	3.8	2.6	1.8	0.9	0.5	0.7	1.4	3.2	0.8	18.6
		(0.8)	(1.0)	(0.7)	(0.5)	(0.2)	(0.03)	(0.2)	(0.9)	(1.9)	(0.3)	(6.5)
N	49	1.4	2.4	2.4	1.7	0.6	0.7	1.1	2.1	2.0	1.0	15.4
		(0.4)	(1.0)	(0.7)	(0.6)	(0.1)	(0.1)	(0.4)	(0.8)	(1.0)	(0.4)	(5.5)
D	53	0.8	1.0	1.21	0.9	0.6	0.6	0.9	1.6	3.2	1.0	11.8
		(0.1)	(0.1)	(0.2)	(0.3)	(0.2)	(0.02)	(0.1)	(0.6)	(1.6)	(0.4)	(3.6)

*Mean no. of *M. Salmonis*
(Mean no. gravid females)